XX. THE BANDED POND-SNAIL OF INDIA (*VIVIPARA BENGALENSIS*).

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(Plates I—III).

PREFATORY NOTE.

In writing this paper our main object has been to provide an introduction to the systematic study of the freshwater Gasteropod molluscs of India. In no single species had the anatomy of the animal been studied in detail, and very little was known about the life-history of any one form. Even for the common European species comparatively little information was available, and there is much indirect evidence that, in bionomics at any rate, considerable differences exist between tropical molluscs and those of temperate climates allied to them taxonomically. In the circumstances a minute comparative study was impossible and we have thought it better, while citing all relevant references to literature available to us, to deal precisely with one species as an isolated unit in the fauna, rather than to generalize on resemblances and differences prematurely. In only one part of the paper has this system been departed from to any great extent, namely in that on the edge of the mantle and the ornamentation of the shell. Here the comparative method was inevitable within the limits of the family, and it so chanced that abundant material was available both from within the limits of the Indian Empire and from a Chinese district on its eastern confines.

Our work has been undertaken in connection with the survey of the freshwater molluscs of India inaugurated at the request of the medical authorities in 1918 by Dr. S. W. Kemp and one of ourselves. There is one point to which we invite attention—that our paper is taxonomic in intention, but could have been prepared only in India and not without a study of the anatomy and bionomics of the species with which it deals. It has been held that systematic zoology is incompatible with bionomics and that different types of mind are necessary in their study. Against such views we protest. They are a libel on taxonomists, if not on taxonomy.

Our thanks are due to the artists of the Zoological Survey of India for the great help they have given us in the preparation of text-figures and plates.

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PART I.—ANATOMICAL.

By R. B. SEYMOUR SEWELL.

The body of *Vivipara bengalensis*, as in practically all Gastero-pod molluscs, is composed of three distinct parts or regions. In the fully-expanded animal the central portion forms a somewhat conical-shaped foot, by means of which the animal is able to crawl over the supporting surface. When fully extended the central aspect of the foot or sole is, roughly speaking, a broad oval, rather broader in front than behind, with a crescentic anterior margin. In young examples the shape of the sole is more elongate and tapers behind to a rounded point. In colour the sole is slate-grey, dotted over irregularly with spots of golden yellow pigment, and just within the anterior margin is a narrow but distinct line of demarkation, indicated by a grey streak, which corresponds to a groove between the more heavily pigmented anterior fleshy border and the less pigmented muscular sole. Above the expanded sole the foot rapidly tapers and on the upper aspect of the posterior region is situated the horny operculum.

The operculum is roughly oval in shape tapering somewhat towards its right side,[1] so as to adapt it accurately to the shape of the mouth of the shell. It is horny in structure and is composed of a number of concentric layers so that it is considerably thicker in the centre, where the opercular muscle is attached, than at the margin, which is often somewhat frayed and irregular in outline. The nucleus is situated excentrically about one-third of the distance from the anterior margin. The colour varies in different regions: around the nucleus it is a deep red-brown and immediately external to this is a narrow band of a pale yellow colour : outside this again the colour often deepens to a golden brown, while the extreme margin is of a blackish tint. The operculum is not absolutely flat, but is somewhat depressed in the central region owing to the pull of the columellar muscle. On the body aspect or lower surface the central portion of the operculum is occupied by the muscular scar to which the opercular muscle is attached. Surrounding this is a smooth ring, which during life is in close apposition to a thin fold of glandular tissue (*vide* Simroth, 1896–1907, pl xviii, fig. 16). In the living animal this fold almost exactly covers the whole of the body surface of the operculum lying outside the scar : owing to the muscle scar being slightly asymmetrical, the fold is somewhat broader on the right side than on the left. It is by the gland cells of this fold that the operculum is secreted.

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[1] In the following description the terms right and left, anterior and posterior, etc., refer to the position in the fully extended condition of the animal.

The main mass of the foot is divided into two layers. The lower layer, which forms the sole and consists of soft greyish-coloured spongy tissue, is traversed by a network of muscle-fibres, which is in turn covered by a layer of columnar epithelium. [It is this tissue that forms the whole surface on which the animal crawls]. The upper and posterior portion of the foot is composed of white muscle-fibres. This mass of muscle, which arises from the operculum, becomes continuous with the columellar muscle, which runs upwards in the floor of the mantle chamber and is inserted into the columella about half-a-turn of the spiral above the mouth of the shell. Between the sole and the opercular muscle is a layer of tissue, consisting of a somewhat open reticulum, the meshes of which enclose numerous irregular spaces, and lying free in these are oval or rounded deeply-staining bodies, which closely resemble starch grains. Similar bodies are also found scattered through the reticulate tissue of the edge of the mantle. Between the two tissues of the foot the pedal nerves and the terminal portion of the cephalic artery pass backwards, and the central region is also occupied by a large venous sinus, running antero-posteriorly in the middle line.

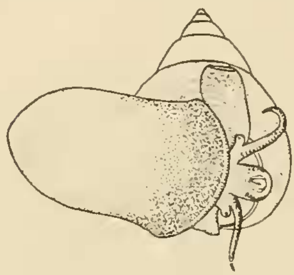

FIG. 1.—Living male of *V. bengalensis* as seen from below.

The anterior part of the body forms a well-marked 'head,' which is produced forwards in the middle line in a short trunk-like snout, on the anterior and central aspect of which lies the oral aperture. Projecting upwards and forwards on either side of the base of the snout is a slender tapering tentacle. Each tentacle arises from a short thick base which is produced on the outer side in a short wide pedicle bearing at its tip a well-marked globular, pigmented eye. Each eye is hemispherical in outline and is situated on the anterior and inner aspect of the pedicle. It consists of a clear cornea superficially, which is usually outlined with golden yellow pigment, and the optic cup is lined by a black, heavily-pigmented retina and encloses an almost spherical lens.

In the female both tentacles are symmetrical, but in the male the right tentacle is somewhat thickened and is curved in a sickle-shaped manner. In this latter sex this tentacle is traversed throughout its whole length by the ejactulatory duct, which opens through a small orifice at the extreme tip. The whole tentacle forms an intromittent organ or penis. Immediately behind and below the base of the tentacles the body surface is produced on either side in a fold—the epipodium. On the left side, the epipodium is triangular or quadrate in shape and is prolonged backwards along the side of the head almost to the point of origin of the mantle. On the right side the epipodium is more complex. Immediately below and to the outerside of the tentacle is a small narrow fold with a rounded anterior margin and a free external border ; this forms a gutter in which the base of the right tentacle and the right eye rest. As we trace the fold forwards and backwards it is seen to commence on the under-surface of the snout close to the junction of the snout and foot ; it then runs backwards along the right side of the snout and near the base of the tentacle it curves outwards and forwards and becomes continuous with the syphon. The syphon is formed by a thin leaf-like process the two edges of which are curved upwards so as to form a tube, which is exhalent in function. The mouth of the syphon looks outwards and downwards and when fully extended, backwards. The inner fold of the syphon is continued backwards and becomes continuous with the branchial fold, which passes backwards and towards the left on the floor of the branchial chamber. The whole of the upper surface of the foot and the head as well as the epipodia and syphon are covered with ciliated epithelium ; the only region devoid of cilia is the clear cornea of the eyes. The head is heavily pigmented with black, variegated with dots and splashes of golden-yellow in varying degrees of intensity. In examples taken from the tank in the Indian Museum compound the snout is frequently an almost uniform black, unrelieved by any lighter pigment and in some cases the tentacles are alternately banded in yellow and black. The syphon is as a rule of a golden colour.

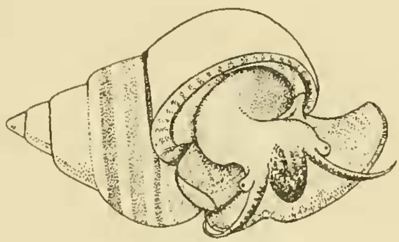

Fig. 2.—Living *V. bengalensis* extended from the shell as fully as possibly.

The part of the body enclosed within the shell is the visceral hump and in a fully-grown example possesses 5½—6 spiral whorls. The skin covering the visceral hump also shows a certain degree of pigmentation, which varies however in different areas as well as in different individuals. In the upper whorls it is often of a deep black colour, while in the lowest or body-whorl the pigment usually follows the lines of the blood sinuses, but as a rule the males are more heavily pigmented than the females. The upper 2½—3 body-whorls are occupied by the liver and the stomach : this latter organ appears on the surface between the lobes of the liver on the right and posterior aspects of the 3rd body-whorl. The penultimate body-whorl, when viewed from above, is seen to be occupied on the left side by a loop of intestine, in front of which is an area of thin skin separating it from the kidney and the upper end of the testis in the ♂ or the albumen gland and shell gland in the ♀. The whole of the lowest or body-whorl is occupied by the branchial chamber, and a series of organs extend throughout its whole length attached to its thin roof. On the extreme left of the branchial roof, running obliquely forward from left to right, is the line of attachment of the gill, and close to it in front and to the left and extending back for only a comparatively short distance from the mantle margin is an opaque whitish-yellow narrow streak, which denotes the position of the osphradium, while extending for the whole distance along its right and posterior border is a brown band, the branchial gland. On the extreme right of the branchial cavity in the ♂ is the crescentic spirally-twisted testis, which is usually of a bright yellow or orange colour, though this character is often obscured by the dense black pigmentation of the skin; in the ♀ this position is occupied by the thin-walled distended uterus, which seems invariably to contain eggs and young in the sexually mature examples, no matter at what season of the year they are taken. To the left of the uterus is a narrow clear line which denotes the course of the ureter, and beyond this again is a broad brownish band, indicating the course of the rectum. The central portion of the roof of the branchial chamber is thin-walled and is traversed by numerous blood-sinuses which commence in the perirectal sinus on the right and pass transversely across to the left to open into the afferent gill vein which runs along the course of the branchial gland. The free edge of the mantle underlies the peristome of the shell, and is thickened and covered with ciliated epithelium. In young specimens it is produced into a series of blunt finger-like processes, which are usually of a golden-yellow colour (*vide infra*). These tend to disappear as age advances, but traces of them can still be made out in the adult. There is often a quite noticeable one situated on the mantle margin opposite the commencement of the gill, and the yellow pigment-splashes on the mantle margin possibly denote the former positions of others that have since disappeared.

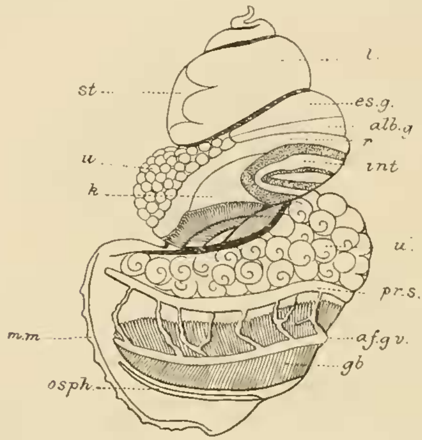

FIG. 3.—*Vivipara bengalensis*: view of the visceral hump from above. *af. g.v.*, afferent gill vein; *alb.g.*, albumen gland; *e.s.g.*, egg-shell gland; *gb.*, gill base; *int.*, intestine; *k.*, kidney; *l.*, liver; *mm.*, mantle margin showing traces of processes; *osph.*, osphradium; *pr.s.*, perirectal blood sinus; *r.*, rectum; *st.*, superficial area of stomach; *u.*, *u'.*, upper and lower parts of uterus.

Immediatly behind the free edge of the mantle, running parallel to it, is the shell-gland. This is most highly developed, as one would naturally expect, during early life, when the rate of growth is most rapid. A similar band exists in *Vivipara vivipara* and has been noticed by Villepoix (1895, p. 513). Laterally the mantle, where it joins the sides of the body, is thickened owing to wing-like expansions of the body muscle which pass outwards and upwards within its substance. Posteriorly the edge of the mantle is continued round the lower aspect of the body; between it and the upper surface of the foot, as a narrow pigmented ridge. Running upwards in the floor of the branchial chamber is the branchial fold. This structure presents a somewhat different appearance in the two sexes. In the female it forms a thin crenated fold, which passes upwards to the extreme apex of the branchial cavity, and finally becomes closely connected with the upper end of the gill immediately in front of the pericardium. Below, it is continuous with the left fold of the syphon and the ridge passing forwards beneath the right tentacle on the right side of the snout. Throughout its whole length it bears on its right side a small subsidiary ridge or fold, which is usually of a brown colour and which lodges a blood sinus. In the male the ridge consists of a stout basal portion, which is surmounted by a thin lamella. The reason for this difference in the two sexes lies in the fact that in the ♂ this ridge accommodates throughout almost its entire length the vesicula seminalis. According to Moore (1901, p. 470, note to fig. 1, pl. xxv) in the closely-related mollusc, *Neothauma tanganyikense*, Smith, this ridge serves as a protection for the gill against damage from pressure against the distended uterus and contained young, and is better developed than in *Vivipara vivipara.* It is always a matter of some difficulty to compare living examples of one species with the published descriptions and figures of others, but it seems to me that in *Vivipara bengalensis* this branchial fold is every whit as well developed as in *Neothauma tanganyikense,* and a study of the living animal has convinced me that Moore is wrong in his view of its function. If a fully-expanded example of *V. bengalensis* be examined in the live state, it will be seen that the branchial fold extends vertically, inclining slightly to the right from the floor of the branchial chamber till its upper free border almost if not actually reaches the roof of the chamber, thus dividing the branchial chamber into two almost completely separate parts. On the left of this ridge is a wide cavity the upper and left wall of which is formed by the gill; and a little behind the mouth of the shell, the tips of the gill-filaments are in close apposition to the free border of the fold. A transverse section about half way up the body-whorl shows that the tips of the gill-filaments may actually pass across above the upper edge of the fold and project into the cavity on its right side. The cavity to the right of the branchial fold is never completely occluded by the uterus; there is always a free interval between the two which becomes continuous below with the syphon tube. The ridge is covered with a tall columnar ciliated epithelium, very similar to that covering the gill lamellae and the margin of the mantle. The presence of an equally well-developed branchial fold in the male indicates that Moore's explanation is not the true one and I entirely agree with Cuvier (1817, p. 6) that its function is respiratory, though it is well known that the syphon is exhalent and not inhalent as he supposed (*l.c.*, p. 4).

The middle portion of the mantle is, as has already been mentioned, thin, and by carefully cutting through along this line and everting the two sides we are able to see the various structures contained within the cavity. The left side of the mantle is the same in both sexes. Commencing in the middle line in front and running backwards and to the left is the line of attachment of the gill. This is of the pectinate type and comprises roughly some three hundred filaments. Each filament or plate is of an elongate triangular shape, with a narrow base of attachment and tapering towards its extremity. The basal attached portion is to the left and the free margin of the gill lies towards the right side. Each gill-filament is covered with ciliated epithelium. Immediately on the right and, owing to the oblique course of the gill, a little posterior to it, is a raised, brownish-coloured ridge, the hypobranchial gland, which extends upwards along the whole length of the gill-base. It is covered with a tall columnar epithelium and lying immediately above it is a large blood sinus, the afferent gill-vein, which collects blood from the viscera and conducts it to the gills, where it is aerated. To the left and in front of the gill and extending backwards from just behind the edge of the mantle to a point about one-third the length of the gill is a raised narrow ridge of a whitish yellow colour; this is the osphradium, and from its upper end a narrow white line is continued upwards, parallel to the gill-base as far as the extreme apex of the mantle cavity. As already mentioned, the mantle cavity is divided into right and left halves by the branchial fold. Water entering the mantle cavity passes into the left of this fold, and having traversed the branchial chamber passes out again down the right side and through the syphon. From the position of the osphradium, which commences a little to the left of the middle line and runs outwards and backwards on the left and in front of the gill, it is evident that all the water entering the cavity must first pass over the osphradium before it can reach the gill-filaments. The osphradium forms a very sensitive sensory organ. It is covered with ciliated epithelium and on its gill-surface it bears a number of small microscopic pits, which are also lined by columnar epithelium. These pits are difficult to see in the natural state, but in some cases indications of them can be made out owing to the mouths being faintly outlined with yellow pigment. The organ is supplied by a special nerve or series of nerves, the osphradial nerves, which arise from the anastomosis between the mantle nerve, coming from the left pleural ganglion and the first gill-nerve arising from the supraintestinal ganglion of the right visceral nerve (for a detailed account of this organ in *Vivipara vivipara* see Bernard, 1890, pp. 244-250).

On the right of the mantle chamber are the rectum and ureter and, in the female, the uterus also. These pass down close together on the right wall of the mantle chamber and open close to the mantle margin in the angle formed by the roof and floor of the cavity opposite the syphon, so that all excreta are at once carried out of the chamber away from the body.

In the female the uterus and ureter open close together. These two ducts run down side by side on the extreme right of the branchial cavity, the ureter being to the left of the uterus, and the rectum lying above and to the inner side of the ureter. The terminal portion of the uterus is known as the vagina: it forms a prominent rounded papilla, the walls of which are thick and spongy, and the orifice is situated at its apex. This orifice is extremely distensile and in the contracted condition is oval or slit-like. The aperture of the ureter lies above and to the outer side of the vagina. It is much smaller and is provided with a sphincter muscle. The rectum passes down above and to the inner side of the ureter, it is continued further forward, towards

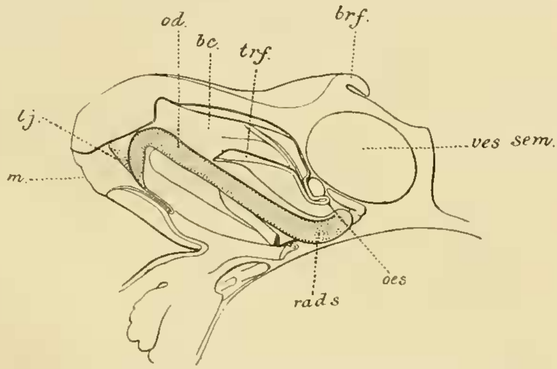

FIG. 4.—*Vivipara bengalensis*, view of the right half of the buccal cavity, cut in the sagittal plane. *bc.* buccal cavity; *br.f.* branchial fold; *l.j.*, lateral chitinous jaw; *m.*, mouth aperture; *od.*, odontophore; *oes.*, oesophagus; *rad.s.*, radular sac; *trf.*, transverse fold above and behind odontophore; *ves.sem.*, vesicula seminalis cut in oblique section.

the mantle margin than either the uterus or ureter and having passed the terminations of these ducts it bends downwards and to the right and opens at the tip of the anal papilla. The terminal papilla and orifice of the anus is usually of a bright golden-yellow colour.

In the male, the rectum and ureter occupy the relative positions as given above, but the position of the uterus is now occupied by the orange yellow testis.

The Alimentary System.

The mouth is situated ventrally at the anterior end of the snout and forms an oval aperture, bounded by fleshy lips, between which the radula is thrust out during the process of feeding with a rotary motion from above downwards. The mouth leads backwards and upwards into the cavity of the buccal mass and each lateral wall is furnished with a low ridge, running from above downwards and backwards. These ridges are yellowish in colour and are armed with a simple chitinous plate. The buccal mass is heart-shaped. In front it becomes continuous with the lips of the mouth, while behind it is produced in two ventral and posterior rounded prominences, between which lie the radular sac below and the oesophagus above. The buccal mass is plentifully supplied with muscles. On cutting through the skin in the middle line of the dorsum of the head and reflecting it outwards, numerous delicate strands of muscle, the protractors, can be seen passing backwards from the sides and dorsum of the skin of the snout to the buccal mass. Below the buccal mass a pair of rather stouter bands passes downwards and forwards to the skin. These are the depressors. The anterior region of the buccal mass is plentifully supplied with intrinsic muscles, as follows:—

(1) Superficially and somewhat towards the ventral aspect on each side is a fan-shaped muscle, which arises by a narrow tendon from the lateral region of the ventral aspect and spreads out fan-wise as it passes forwards to be inserted into the oral tube.

(2) Immediately deep to this is a sphincter muscle, the fibres of which run concentrically around the tube.

(3) A band of muscle, rather narrower behind than in front, arises from the sides of the buccal mass, immediately posterior to the buccal nerve, across which it passes forwards, spreading out to be inserted round the oral tube.

Two pairs of strong muscles, the fibres of which are of a shining white colour in contradistinction to the fibres of the preceeding muscles which have a reddish tinge, arise from the main muscle mass of the body and pass forwards to be inserted into the buccal mass. These are the anterior and posterior retractors:—

(4) The anterior retractors are inserted into the anterior ventral aspect of the buccal mass by narrow tendons; passing backwards side by side they cross the pedal commissure dorsally and can be seen to arise from the main muscle mass near the base of the antennae.

(5) The posterior retractors arise from the main muscle mass and pass forwards and slightly upwards external to the pleuro-pedal commissure of the central nervous system. Here each gives off a slip to the lateral wall of the oesophagus. It then continues forwards internal to the cerebro-pedal commissure and finally joins the side of the buccal mass as a fine tendon which can be traced forwards below the buccal ganglion and ends in a delicate expansion internal and deeply to the muscle (3) noted above. These two muscles are not quite symmetrical for that of the left side arises from the main muscle mass of the body at a higher level than that on the right.

A series of small muscle strands, usually three in number, arise close to the origin of the above muscle and pass forwards and upwards to be inserted into the surface of the radular sac.

The upper wall of the buccal mass is thin and on cutting through it in the antero-posterior line we get a view of the buccal cavity. In the middle line in front arising from the floor is a stout pyriform mass the narrow end of which projects upwards and forwards; this is the odontophore and it can be seen to carry the radula which disappears posteriorly into the radular sac. The radula is a yellowish narrow ribbon, which carries a series of small spinose teeth. These teeth are divided according to their position and dentation into three series. In the middle line is the median row, consisting of a single central tooth. as it is called. The anterior border of this tooth is recurved and is cut into a series of denticles. There is a wide rounded median denticle and five smaller triangular denticles on either side. On each side of the central tooth are a pair of laterals. In both cases we get the rounded median denticle and a series of smaller triangular or claw-like denticles on each side of it.

FIG. 5.—Radular teeth of *V. bengalensis.*

As a rule there are five of these claw-like denticles on either side of the median denticle in each of these teeth, but occasionally we find that there are six denticles on the outer side of the second lateral tooth. This variation may occur in a portion of a radula the rest of which shows the normal condition. The marginal tooth is usually curved inwards towards the middle line, and bears on its margin a uniform series of small denticles. In some cases as in the radula figured, there may be a broad sharp extra denticle at the extreme margin. The radula of *Vivipara bengalensis* was figured by Fischer (1887, fig. 499, p. 732), but a comparison of his figure with that given above will render unnecessary any apology for refiguring it here.

Lying behind and above the odontophore is a transverse fold with a crescentic anterior margin, the median portion of which is somewhat thickened and is slightly notched. Each lateral wall of the buccal cavity is thick and swollen and contains a cartilaginous mass—the odontophoral cartilage. Each cartilage is roughly oval in shape, the anterior end being somewhat more sharply rounded than the posterior, and is concavo-convex, the concavity being towards the middle line. The lower border is thin and is curved inwards. From the outer aspect a little below and behind the centre of the cartilage numerous muscle-fibres arise and spread out in the lateral walls of the buccal mass. At the posterior end of the buccal mass beneath the oesophagus lies the radular sac, in which the radular ribbon is secreted. It is a short stout tube having a somewhat dorsally directed nipple-like posterior end. Above the odontophore the cavity of the buccal mass is hour-glass shaped the upper portion having a very thin-walled roof. Opening into the cavity are the ducts of the salivary glands.

The salivary glands are irregular asymmetrical racemose glands, consisting of a number of branching and anastomosing lobules. It is impossible accurately to separate the gland into right and left portions, and hence in this respect *Vivipara bengalensis* offers a marked contrast to *Neothauma tanganyikense* in which the salivary glands are separate and form compact lobulated masses (vide Moore, 1901, fig 2, pl. xxv). The main mass of the salivary gland lies on the dorsal side of the oesophagus behind the central nervous ring and is intimately bound up with the supra-oesophageal nerve as it crosses the oesophagus from right to left. A pair of delicate narrow salivary ducts arise anteriorly and pass forwards beneath the cerebral commissure.

The oesophagus is thin-walled and usually presents a greenish appearance due to its contents. It passes backwards and to the left and then turns towards the right again to pass up the columellar aspect of the visceral hump. During its course backwards in the floor of the branchial cavity it lies beneath the branchial fold and above the main muscle mass: on its left side lies the supra-intestinal nerve, and during this part of its course it lies in a well-marked venous sinus and is in close relationship to the cephalic aorta. At the posterior end of the mantle cavity the oesophagus passes upwards in the floor of the pericardial chamber and so reaches the liver. Finally in the upper part of the visceral hump the oesophagus curves round and opens into the stomach. This is a wide cavity occupying the third and fourth whorl. On cutting away the superficial wall of the stomach the cavity is seen to be incompletely divided into three regions, of which the upper two represent the cardiac portion of the stomach, while the lower part is the pyloric cavity. The junction of oesophagus and stomach is marked by a crescentic fold, just beyond which lies the orifice of the duct from the upper lobe of the liver. On the inner aspect, and dividing the cardiac region into two, is a broad longitudinal fold which passes downwards, and which carries a well-marked blood vessel. Below, this ridge divides into right and left folds which diverge and form the line of separation between the cardiac and pyloric regions. In the right half of the cardiac chamber the wall of the stomach is thrown into a series of longitudinal parallel folds, each fold being marked with a brown streak. The lower portion of this cavity is lined by a thin layer of chitin, which becomes thicker and more marked over the ridge separating the cardiac and pyloric cavities.

The pyloric portion of the stomach is a wide cavity that gradually tapers towards its lower end. Running across the posterior wall is a doube fold, of which the upper lip is often much more prominent than the lower. Between these two folds is a narrow gutter into which the ducts of the right and left lobes of the liver open. The junction of stomach and intestine is very clearly defined owing to the different character of the lining mucous membrane. The stomach is lined by tall columnar ciliated cells, which give the wall a soft velvety appearance, whereas the intestinal wall has a yellowish colour and is lined with a layer of chitin which gives it a smooth bluish metallic look.

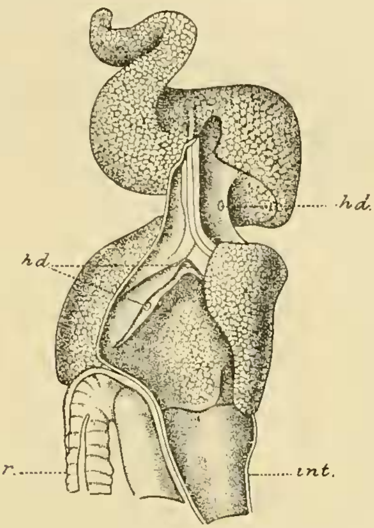

FIG. 6.—*Vivipara bengalensis*, view of inner wall of gastric cavity after removal of superficial wall. *hd.*, openings of hepatic ducts; *int.*, intestine; *r.*, rectum.

The liver, owing to the bulging of the stomach on its outer surface and the passage through it internally of the oesophagus, is incompletely divided into three lobes, an apical, occupying the upper turns of the spire, and a right and a left lobe inferiorly. The organ has a golden brown colour, which is, however, frequently obscured owing to heavy pigmentation of the overlying skin. It is a racemose gland, with elongate acini the tips of which reach the surface. Each acinus is hollow and is lined with a columnar or cubical epithelium. Each lobe is furnished with a separate duct, that of the upper lobe opening into the left part of the cardiac portion of the stomach, while the ducts of the right and left lobes open on the posterior wall of the pyloric cavity between the folds noted above. According to Leydig these folds probably serve to regulate the flow of bile.

The intestine passes forwards and to the right in the penultimate body-whorl and then turns sharply back again, forming a loop which overlies the pericardial cavity. In the first part of its course the lumen gradually narrows: it is lined by a yellow-coloured epithelium covered with a thin chitinous layer and running along its posterior aspect is a gutter with fleshy lips which are pigmented brown. At the apex of the loop, the character of this gutter becomes somewhat modified and the right-hand fold becomes proportionately larger and now appears to form a longitudinal ridge or typhlosole projecting from the posterior wall. The intestine having again reached the liver turns sharply forwards once more and is now continued on as the rectum. It passes forwards on the right of the whorl, lying on the surface; in the ♀ it is in close apposition to the albumen- and shell-glands, and passes downwards and forwards immediately to the outer side of the kidney and the first part of the ureter. In the body-whorl it passes forwards, as we have already seen, in the roof of the branchial chamber and opens at the anus. In this latter part of its course its walls are thrown into numerous transverse folds. The contained faeces are moulded into small oval compact masses.

The Vascular System.

The heart lies in the pericardial chamber at the apex of the branchial cavity and on the inner side of the penultimate body-whorl. It is a closed cavity the walls of which are in places extremely thin and delicate and hence are very liable to become torn or ruptured. On its inner aspect the pericardium is separated from the shell only by thin membrane; above and in front it is bounded by the kidney, and above and behind is the loop of the intestine and the liver; on its right or outer side lie the genitalia and the rectum; while below it lie the oesophagus, the termination of the supra-intestinal and sub-intestinal nerves and the splanchnic ganglion and, in the female, the loop of the oviduct. On its outer and upper aspect the cavity of the pericardium communicates with the kidney through the reno-pericardial opening, the position of which will be studied when dealing with the kidney itself.

The heart consists of two chambers. Anteriorly is the soft-walled whitish-looking auricle, the walls of which are usually thrown into a series of irregular folds. In almost every adult example examined, the auricular wall was seen to contain a number of small round white bodies. These are cysts of an Echinostome Agamodistome and are present in such large numbers that they may almost fill the whole organ. The wall of the auricle is thick and glandular, and is said to form the haematic gland that is present in other molluscs (*vide* Perrier, 1889, p. 178). The ventricle lies posteriorly and is a rounded body of a pale brownish colour and its walls are thick and muscular. The auriculo-ventricular aperture is tube-like and projects into the cavity of the ventricle. From the inferior aspect of the ventricle arises a short wide aorta. In *Vivipara vivipara* (*vide* Perrier, 1889, pl. viii, fig. 38 x.) there is said to be a valve-like flap at the point of origin of the aorta from the ventricle, which prevents the regurgitation of blood during the ventricular diastole. Leydig (1850, p. 170) on the other hand states that there is a cresentic valve situated between the auricle and ventricle. In *Vivipara bengalensis* I have failed to find any indication of either. The common aorta almost at once bifurcates into two wide trunks, which run in opposite directions. One branch, the *cephalic aorta,* passes forwards and downwards to the inner side of and close to the oesophagus. In this position it passes forwards below the floor of the mantle cavity and high up in the chamber it gives off a large branch that diverges towards the left side and, where the mantle margin merges into the foot, breaks up into branches. The main trunk of the cephalic aorta is continued on, crossing beneath the oesophagus to reach its right side. In this situation it has the sub-intestinal nerve, lying in a blood sinus, on its right and in the ♂ the vesicula seminalis lying directly above it. At the anterior end of the branchial chamber it comes into relationship with the radular sac, and passes forwards on its right side. It then dives ventrally, and below and behind the pedal commissure it gives off a branch to the snout and then divides into anterior and posterior branches which run to the respective regions of the foot. Throughout its course beneath the branchial chamber it gives off a number of fine branches to the muscles of the body.

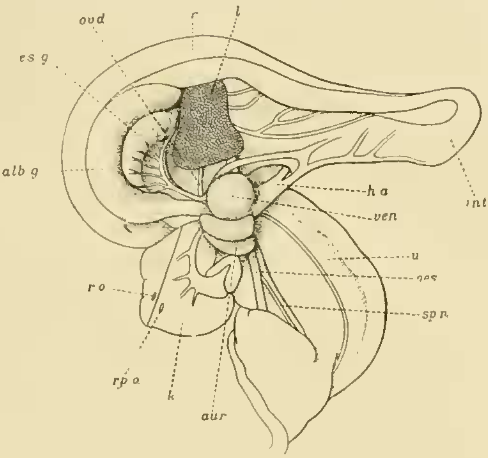

FIG. 7.—*Vivipara bengalensis*, view of the pericardial chamber. The loop of intestine has been turned over to the left side and the kidney downwards and to the right. *alb.g.*, albumen gland; *aur.*, auricle; *es.g.*, egg-shell gland (receptaculum seminis); *h.a.*, hepatic aorta, *int.*, intestine; *k.* kidney; *l.*, liver; *oes.*, oesophagus; *ov.d.*, oviduct; *r.*, rectum; *r.o.*, renal orifice into ureter; *rp.o.*, reno-pericardial opening; *sp.n.*, supra-intestinal nerve; *u.*, uterus; *ven.*, ventricle.

The *hepatic aorta* passes upwards and backwards in the floor of the pericardial cavity, immediately to the left of the oesophagus. It almost at once gives off a large branch which passes at first slightly inwards and upwards to reach the lower wall of the intestine, where it subdivides into two main branches. One of these curves forwards and runs along the under aspect of the first part of the intestine, supplying branches to it, and the main vessel passes at first forwards as far as the bend of the intestine and then continues on along the second part of the intestine, lying immediately beneath the typhlosole-like ridge on its under aspect. The other branch curves forwards and to the right, crossing behind the oesophagus, and sends branches to the testis in the ♂. In the ♀, after supplying branches to the albumen and shell glands, curves backwards and to the left and reaches the wall of the uterus where it finally divides into ascending and descending branches, the latter of which is much the longer and larger of the two and runs down the ventral wall as far as the point where the wing-like expansion of the body muscle meets the mantle margin. The main hepatic artery is continued upwards between the liver and stomach, where we have already noticed it lying in the longitudinal fold on the posterior wall of the cardiac portion of the stomach, and ends in branches supplying the liver in the apical whorls.

The venous system consists very largely of wide spaces or sinuses, whose walls are very thin and in consequence are very difficult to define. Occupying the central portion of the foot, between the dense white muscle and the grey spongy tissue of the sole, is a wide irregular sinus, the blood from which, according to Leydig, passes upwards and backwards to reach the venous sinus on the ventral posterior aspect of the kidney. This sinus appears to be joined at the left posterior angle of the kidney by a venous sinus, which runs up the right side of the branchial fold in the floor of the mantle cavity, and it is also joined by a sinus crossing from right to left along the posterior and upper margin of the kidney and having its origin in the perirectal sinus. The conjoined vessel passes down superficially on the left side of the kidney between it and the branchial gland. This vessel is known as the afferent gill-vein. Lying to the right of the kidney in the body-wall is a large sinus which receives blood from the organs lying in the upper coils of the visceral hump; this passes downwards and at the apex of the kidney joins the afferent gill-vein that we have already seen passing down the left margin along the branchial gland. The afferent gill-vein can be traced down the whole length of the branchial gland on the right of the gill-base almost as far as the mantle margin; below the level of the kidney it is joined by a further series of small branches which arise from the perirectal sinus and pass across the thin median portion of the mantle roof. The perirectal sinus also received tributaries in the female from the wall of the uterus. The afferent gill-vein supplies branches to the gill-filaments and the blood after being aerated returns to the efferent gill-vein which lies on the left side of the base of the gill; this vein passes from below upwards and at the apex of the mantle cavity opens into the cavity of the auricle. A large vein runs down beneath the floor of the branchial chamber on the right side of the oesophagus. Superiorly it receives tributaries from the liver, and in the ♀ from the albumen gland and egg-shell gland while a large branch passes up on the inner aspect of the uterus and then crosses over behind the sub-intestinal nerve to join it near the apex of the branchial cavity.

The Renal System.

The kidney is a triangular pyramidal organ of a pale greenish colour, lying in the roof of the mantle cavity at its extreme apex. Along the external or right margin runs the rectum and the perirectal blood sinus, below which lies the commencement of the ureter, while along the left or inner margin is the commencement of the afferent gill-vein and the base of the gill. The posterior border is connected with the loop of the intestine by an intervening fold of thin membrane. Of the four surfaces of the kidney, the upper lies just under the skin against the shell. The apex of the kidney lies to the front, and the left surface forms the upper part of the right-hand wall of the mantle cavity and is in close relationship with the terminal portion of the branchial fold. The base of the kidney, which is triangular in shape with the apex of the triangle directed ventrally, faces backwards towards the upper part of the visceral hump and forms part of the anterior boundary wall of the pericardial chamber. The right surface of the kidney is in relationship with the upper part of the ureter, which separates it from the testis in the male or the uterus and shell-gland in the female. A thin fold of membrane passes outwards and backwards from the right-hand border of the base of the kidney to the testis in the male and the shell-gland in the female and forms the upper boundary limit of the ureter.

The kidney is provided with two orifices that open respectively into the ureter and the pericardium. Both these apertures are situated close together near the right posterior border. The reno-pericardial opening is situated on the posterior or pericardial surface of the kidney near the supero-external angle: it is oval in shape and has thin walls. The external or ureteral orifice is situated on the external surface, close to the reno-pericardial aperture, but separated from it by the conjoined pericardium and wall of the ureter. It possesses thick protuberant lips, which are covered with ciliated, columnar epithelium and are often marked by a ring of black or brown pigment. The ureter is a thin-walled tube having in cross section a triangular lumen. Its right wall is bounded by the testis in the male or the uterus and part of the albumen- and shell-glands in the female: the left wall is thin and separates it from the branchial chamber, while its upper or superficial wall is formed partly by the rectum and perirectal blood sinus and a thin-walled portion in contact with the superficial skin. The orifice of the ureter lies, as we have already seen, near the right-hand margin of the mantle edge, in the angle between the rectum and the vagina in the female, or in the corresponding position to the left and above and behind the anus in the male.

The Genital System.

Vivipara bengalensis like all members of the genus is diœcious, or in other words the two sexes are separate. We have already seen that sexual differences are apparent in the structure of the right tentacle, which in the male is thickened and recurved and acts as a penis or intromittent organ. This change does not seem to have proceeded quite as far in *Vivipara bengalensis* as in the European species *Vivipara vivipara*, for in the former the modified tentacle is sickle-shaped, whereas in the latter it is figured as being completely contracted up into a rounded projection (*vide* Fischer, 1887, fig. 501, p. 733), which may actually be enclosed in a small pocket (*vide* Baudelot, 1863, p. 218, pl. v, figs. 14–15).

♂. The testis in *Vivipara bengalensis* forms a compact semilunar organ lying on the right of the branchial chamber, and occupying the same position as the uterus in the female. It is of a bright orange-red colour and extends to the upper end of the branchial cavity, where its apex is in close relationship with the pericardial cavity and is connected by a thin fold of membrane with the lower surface of the liver. The gland is flattened from side to side, the right surface being in contact with the shell while the left surface forms in part the right wall of the ureter and below this the right wall of the mantle cavity. In possessing a testis formed of a single mass in this position in the body *Vivipara bengalensis* differs markedly from *Vivipara vivipara*, in which the testis consists of two distinct portions, the upper occupying the extreme apex of the visceral hump and the lower lying at the lower margin of the liver between the stomach and the coil of the intestine (*vide* V. Siebold, 1836, p. 241, and Simroth, 1896-1907, pl. xliii, fig. 9; also Erlanger, 1891, pp. 665-666).

Although the testis in *Vivipara dissimilis* (Müller) occupies the same position as in *V. bengalensis*, it differs in having a more or less quadrilateral extension from its upper pole, which passes upwards on the outer side of the pericardial cavity and abuts against and is firmly united to the lower aspect of the liver, from which, however, it can be readily recognised by its golden orange colour. This upward expansion is clearly demarcated off from the rest of the organ, which closely resembles the whole testis of *V. bengalensis*, and partakes more of the nature of a second lobe. *V. dissimilis* in this respect is intermediate between *V. vivipara* and *V. bengalensis*.

A series of narrow delicate ducts, the vasa efferentia, arise from the lower border of the testis and passing respectively upwards and downwards along its lower border converge to form a narrow tube, the vas deferens, which passes to the left beneath the floor of the branchial chamber, crossing above the sub-intestinal nerve, to reach the vesicula seminalis. The first part of the vas deferens is sometimes dilated to form a spindle-shaped swelling, but the portion of the duct near the vesicula seminalis is narrow. The vesicula seminalis forms a wide tube which passes downwards and forwards from just in front of and below the pericardium to the base of the right tentacle beneath the floor of the branchial chamber approximately in the middle line and exactly beneath the branchial fold. The upper portion of the organ curves round to the right to meet the vas deferens. The whole organ is pigmented and possesses an iridescent appearance like mother-of-pearl. Cuvier (1817, p. 7) described this structure in *V. vivipara* as the copulatory organ, but Treviranus subsequently referred to it as a seminal vesicle, and there seems to be some doubt as regards its true function. Later authors refer to it either as the vesicula seminalis or the prostate gland. Erlanger

(1891, p. 665), appears to consider it to be an ejaculatory duct, in which view Simroth (1896–1907, note to fig 9, pl. xliii) concurs. Baudelot (1863, p. 217), on the other, hand seems to consider that it is of the nature of a prostate gland, and describes the internal surface as consisting of a series of transverse lamellae, running parallel to each other. In *V. bengalensis*, this region of the duct is surrounded by a layer of circular connective tissue fibres and the lining mucous membrane is thrown into folds as described by Baudelot, though these are narrower and more numerous than he figures them. A transverse section shows that these folds are supported by a connective tissue lamella, on each side of which is a layer of cubical epithelium. The whole organ is glandular in character and is in my opinion a 'prostate' gland. The terminal portion of the male duct is comparatively narrow. It passes up the right tentacle and opens by a small orifice at its extreme tip. In this part of its course the duct-wall is thick and muscular, and constitutes an ejaculatory duct.

According to Smith (1881, p. 221) the right tentacle of the male *Vivipara vivipara* is merely the sheath of a true penis, "which, at the time of copulation, protrudes through it." As regards this statement he appears to be at variance with other authors. Simroth (1896–1907, p. 617) states that the short 'penis' can be coiled up in a pouch of skin at the outer side of the tentacle, and Baudelot (1863, p. 218, pl. v, fig. 14) shows this condition very clearly. It is this coiled up portion of the tentacle which is the 'penis,' and no portion of the genital duct is protruded through it during the act of copulation, for, as Baudelot points out, the terminal portion of the duct, which I have considered to be an ejaculatory duct, is intimately connected with the skin of the tentacle and could not possibly be everted. In this respect *Vivipara vivipara* and *V. bengalensis* appear to be identical. In this latter species the terminal portion of the ♂ genital duct is closely bound to the skin of the tentacle by connective tissue. I have not been able to observe the act of copulation, but the structure of the right tentacle in this species shows that here also it is the tentacle itself which is the intromittent organ.

The seminal fluid contains two quite distinct forms of spermatozoa. The first form, which appears to be that of the mature functional spermatozoon, consists of an elongate spiral head, with 6–7 turns in the spiral and of a refractile appearance : behind this is a single long flagellum. The second form is usually described as 'worm-shaped'; it may be straight or spirally twisted, is much stouter than the spiral kind and terminates in a tuft of numerous short flagellae. From the time of their discovery these two forms of spermatozoa have interested zoologists and accounts of them and their mode of development have been given by V. Siebold (1836), Leydig (1850), Baudelot (1863), Simroth (1891–1907) and others, but we are still ignorant of the function of the worm-shaped type.

♀. The genital organs of the female *Vivipara bengalensis* appear to agree exactly with those of *V. vivipara.* One of the best accounts of these organs is that given by Baudelot (1863, pp. 218–220, pl. v, figs. 16–20). Erlanger (1891, p. 664) in his description claims to have followed Baudelot and to have reproduced his illustration of this system. But a comparison of the two figures serves to show how misleading the results of such a procedure may be, for Erlanger (*l.c.*, fig. 3) shows no trace of the duct of the albumen gland, though this is clearly seen in Baudelot's figure (*l.c.*, fig. 16).

In *Vivipara bengalensis*, the ovary consists of a few small scattered follicles along the commencement of the oviduct. It is of a red-brown colour and so in spite of its small size can be distinguished from the liver tissue: it lies in the third body-whorl, in close contact with the posterior wall of the cardiac region of the stomach and along the course of the hepatic artery. The various follicles contain numerous small ova, which have a diameter of 0·021-0·025 mm. The oviduct passes downwards as a fine tube, also of a red-brown colour, to the lower margin of the liver and is then continued on along the floor of the pericardial cavity on the right of the oesophagus. At this point it is joined by the short wide duct of the albumen gland. This gland is situated just below the skin on the right of the pericardium. It is connected by a thin fold of membrane with the loop of the intestine on the upper surface of the pericardium and the rectum passes forwards and downwards along its superficial aspect, which is grooved to receive it. Below, the gland is intimately bound down to the U-shaped egg-shell gland, or receptaculum seminis as it is usually termed. The albumen gland is tongue-shaped and slightly curved. It is of a bright orange-red colour and its apex is in contact with the lower surface of the liver. From its inner and posterior border a wide duct arises which passes backwards internal to the first part of the egg-shell gland and joins the oviduct. The combined duct is then continued downwards and inwards for a short distance and then turns back again towards the apex of the visceral hump. This portion of the duct is of a brown colour and it can be traced to the lower and inner limb of the egg-shell gland, into which it opens at its extreme end on a smooth rounded papilla.

The egg-shell gland is, as already mentioned, a wide U-shaped tube the walls of which have a yellow-brown colour very similar to that of the liver. The ascending limb of the U is at first narrow, but as it passes upwards towards the liver it gradually dilates and then turns sharply round on itself and passes downwards again on the right of the ascending limb and in close contact with the shell. On opening the tube, the inner wall is seen to be thick and glandular and is thrown into a series of folds. At first these folds run parallel to the length of the tube, but as we trace them up they become more and more oblique curving towards the right and in the descending limb of the gland they run spirally. On the posterior aspect of the descending limb a smooth whitish ridge with a gutter on its right side can be seen to arise at the upper and posterior end, passing downwards to the orifice through which the shell-gland opens into the uterus. At this point the smooth ridge becomes continuous with a longitudinal fold, which, as we shall see later, passes down the whole length of the lower wall of the uterine cavity. I have throughout referred to this **U**-shaped portion of the genital duct as the egg-shell gland. In the earlier descriptions of *V. vivipara*, such as that given by von Siebold (1836 p. 244), it is referred to as a receptaculum seminis, because free spermatozoa were found in the contents. That it serves as a repository for semen is beyond doubt, but it seems to me that its true active function is to produce the thin membranous covering which surrounds the eggs. The egg-shell gland opens below by a wide crescentic mouth into the thin-walled uterus. This is a wide cavity, which we have already seen lying on the right of the mantle cavity throughout the whole length of the body-whorl. It invariably contains eggs and developing young when once sexual maturity has been reached. Running along the whole length of the floor of the uterine cavity is a double fold of opaque-white colour which is in marked contrast with the thin translucent side walls This double fold has a narrow base of attachment and the left-hand or inner fold is thin and convoluted while the outer fold is thicker and has a straight margin. This outer fold is covered with a ciliated epithelium and beneath this fold, between it and the floor, the seminal fluid, which has been introduced by the male is conducted up to the shell gland. The terminal portion of the genital duct is comparatively narrow and thick-walled. It opens on the right of the branchial chamber by an oval orifice, the vagina, which is situated terminally on a small papilla. During copulation the right antenna of the male is introduced through this orifice and the seminal fluid is deposited within the uterus.

The members of the genus *Vivipara*, as their name implies, produce live young, but they are actually ovo-viviparous. If we examine the contents of the uterus during the breeding season we find that the lower region of the duct contains numerous young, with 2½ turns in the shell, ready to be born, but as we pass further and further upwards the state of maturity of the young becomes less and less, until at the extreme upper end we find large ova containing an extremely minute embryo, with only half a turn in the spiral of the visceral hump. These eggs are large and are pyriform or globular in shape. They are surrounded by a thin delicate membrane, which at one point is twisted up and produced into a kind of free pedicle. Filling the whole egg, and surrounding the young embryo is a mass of faintly blue albuminous material, which under the higher powers of the microscope, can be seen to contain large numbers of spermatozoa, so that it would appear that the seminal fluid of the male serves the double function of fertilizing the ovum and providing in part for the nourishment of the embryo. In addition to the spermatozoa we find numerous fine spicules which dissolve readily on the addition of glacial acetic acid and are presumably calcareous in nature. It is probably from these spicules that the young embryo derives the calcareous substance necessary for the production of the shell.

The Nervous System.

A very full and complete account of the nervous system of *Vivipara vivipara* has been given by Bouvier (1887, pp. 63-72, pl. iv, figs. 15, 16) and that of *Vivipara bengalensis* agrees in almost every particular, so far as I have been able to ascertain. The type of nervous system is that known as 'dialyneurous,' in that the connection between the sub-intestinal nerve and the right pleural or parietal ganglion is an indirect one, brought about by the union of a branch arising from the right pallial nerve and a branch from the sub-intestinal nerve. A similar anastomosis exists on the left side of the body, between the left pallial nerve and a branch from the supra-intestinal ganglion. Moore (1903, p. 276) has distinguished three different types of nervous system, based on the relative positions of the three main ganglia of the central nervous system—those forms of nervous system in which, as in *Vivipara*, "the pleural ganglia are more or less half-way between the cerebrals above and the pedals below the oesophagus" he terms 'dystenoid.'

The cerebral ganglia are situated in the base of the snout on either side of the commencement of the oesophagus, immediately behind the buccal mass. Each ganglion is roughly triangular in shape, with the base posteriorly and the apex pointing forwards and outwards. On the external aspect a shallow groove divides the ganglion into two parts, an anterior 'labial' portion and a posterior 'cerebral' portion. Each ganglion is of a red-brown colour and is connected with its fellow across the dorsal aspect of the oesophagus by a wide, short cerebral commissure. The ducts of the the salivary glands pass forwards close to the middle beneath this commissure and above the oesophagus. The 'labial' portion of the cerebral ganglion is flattened dorso-ventrally and from its outer and antero-internal borders a number of nerves arise. From the antero-internal border two fine nerves arise close together and pass forwards over the dorsum of the buccal mass to the skin of the snout. Near the apex of the ganglion, but still from the inner border, a stout nerve arises and passes forwards on the side of the buccal mass to the snout and lips. At the extreme apex of the ganglion three nerves arise close together: (i) this runs forwards on the side of the buccal mass to the lips and snout; (ii) this is the stoutest of all three and is the buccal nerve. It first passes downwards and forwards on the lateral aspect of the buccal mass towards the ventral aspect: here it turns upwards and passes deep to the lateral retractor muscle of the lips, and just above and behind the origin of this muscle from the side of the odontophoral cartilage it ends in a rounded or triangular yellowish-brown body, the buccal ganglion, which lies just in front of and below the point of entrance of the salivary duct into the buccal cavity.

From each buccal ganglion three nerves arise, two of these pass obliquely upwards towards the dorsal aspect of the buccal mass, but the third and largest passes backwards and downwards around the posterior aspect of the buccal mass, below the oesophagus and above the radular sac to the ganglion of the opposite side. This is the buccal commissure. (iii) This nerve arises just external to the buccal nerve and passes forwards and downwards to the lower part of the lip of the mouth ; it gives off a branch which passes

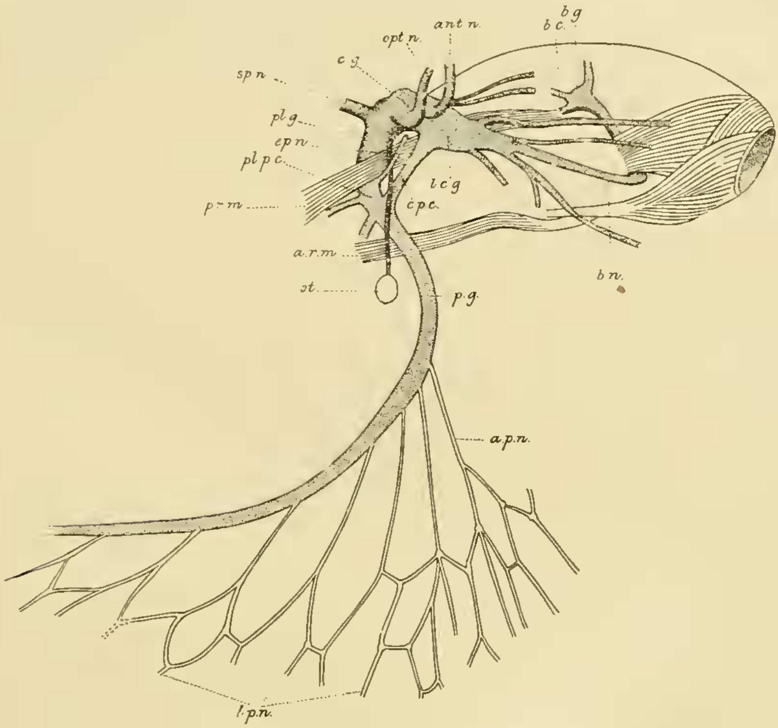

FIG. 8.—*Vivipara bengalensis*, nervous system of the right side. *ant n.*, antennal nerve ; *a.p.n.*, anterior pedal nerve ; *a.r.m.*, anterior retractor muscle of buccal mass ; *b.c.*, buccal commissure ; *b.g.*, buccal ganglion ; *b.n.*, buccal nerve ; *c.g.*, cerebral ganglion ; *c.p.c.*, cerebro-pedal commissure ; *e.p.n.*, epipodial nerve ; *l.c.g.*, labial portion of the cerebral ganglion ; *l.p.n.*, lateral pedal nerves ; *opt.n.*, optic nerve ; *ot.*, otocyst ; *p.g.*, pedal ganglion ; *p.r.m.*, posterior retractor muscle of buccal mass ; *pl.g.*, right pleural ganglion ; *pl.pc.*, pleuro-pedal commissure ; *sp.n.*, supra-intestinal or right parietal nerve.

across below the oral tube, joining with its fellow of the opposite side to form the labial commissure. Three nerves arise from the rounded upper and outer aspect of the cerebral portion of the cerebral ganglion. From the upper aspect a stout nerve, the antennal nerve, arises and passes forwards and outwards to the antenna; although in the male the right antenna serves the double function of a tactile organ and the intromittent organ, the nerve that supplies it shows no obvious increase in size. From the posterior and outer surface of the ganglion the optic nerve arises and passes forwards and outwards external to the antennal nerve and ends in the sensory epithelium of the eye. As we trace this nerve backwards to the brain it can be seen to end in a quite distinct rounded swelling which forms a localised prominence on the external and posterior margin of the cerebral ganglion. From the side of the cerebral ganglion immediately below the origin of the optic nerve a small nerve arises, which can be seen to pass directly downwards. This small branch, which is the nerve to the otocyst, passes down external to the lateral retractor muscle of the buccal mass and the pedal ganglion and finally ends in the otocyst, which lies a little behind and to the outer side of the pedal nerve

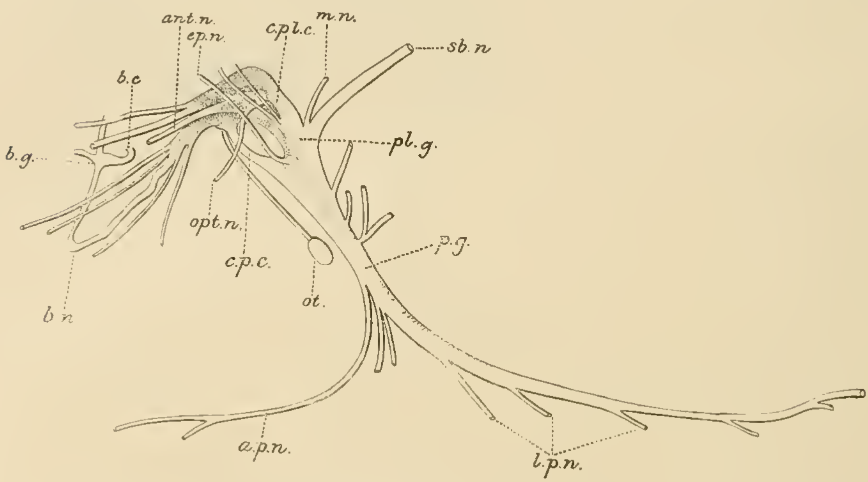

FIG. 9—*Vivipara bengalensis*, nervous system of the left side. *ant.n.* antennal nerve; *ap.n.*, anterior pedal nerve; *b.c.*, buccal commissure; *b.g.*, buccal ganglion; *b.n.*, buccal nerve; *c.p.c.*, cerebropedal commissure; *c.pl.c.*, cerebro-pleural commissure; *e.pn.*, epipodial nerve; *l.p n.*, lateral pedal nerves; *opt.n.*, optic nerve; *ot.*, otocyst; *p.g.*, pedal ganglion; *pl.g.*, pleural ganglion; *sb n.*, sub-intestinal or left parietal nerve.

close to its origin. Each otocyst is a small oval sac, the long axis of which is vertical; it has a shining refractile appearance and its cavity is filled with a number of small calcareous concretions of varying shape, the otoliths. [For more detailed descriptions of this organ, the reader is referred to the accounts given by Leydig (1850), and Lacaze Duthiers (1872).] The position of the pleural ganglia and consequently the arrangement of the nerve commissures that arise from the cerebral ganglia differ on the two sides of the body. On the left side, the pleural ganglion lies mid-way between the cerebral and pedal ganglia and the arrangement of the ganglia and commissures conforms to Moore's definition of the 'dystenoid' type of nervous system. On this side of the body two commissures, that differ markedly from each other, arise from the ventral aspect of the hinder portion of the cerebral ganglion. The anterior cerebro-pedal commissure is long and narrow and of a white colour; it passes downwards external to the lateral retractor muscle of the buccal mass to join the pedal ganglion. The posterior cerebro-pleural commissure is broad and ribbon like, and can be seen to consist of two parts, an anterior brownish-coloured portion and a posterior white portion. Inferiorly it fades into a very ill-defined left pleural ganglion. Below this ill-defined ganglion a short broad commissure passes downwards, being joined by the cerebro-pedal commissure to the pedal ganglion. On the right side of the body there is no distinct cerebro-pleural commissure. The right pleural ganglion lies close against the posterior end of the cerebral ganglion and is only separated off from it by an ill-defined neck. The pleuro-pedal commissure is in consequence proportionately long. On this side of the body the arrangement of these ganglia conforms to what Moore (1903, p. 276.) terms the 'epiathroid' type of nervous system.

From the pleuro-pedal commissures several fine nerves arise; of these one, usually the largest, can be seen to arise from the commissure low down near its point of union with the cerebro-pedal commissure. This is the epipodial nerve and that on the left, which is usually slightly the larger, supplies the epipodium on that side, while the right supplies the fold beneath the right tentacle and the inner or left half of the syphon. The other nerves pass upwards and outwards to the tissues at the base of tentacle. The pedal ganglia are long ribbon-like structures of a brown colour, which are connected above with the cerebro-pedal and pleuro-pedal commissures. Each of these ribbons is composed largely of ganglionic nerve-cells, and in consequence the whole length of the structure must be regarded as being homologous with the more compact pedal ganglia of other molluscs. Immediately beneath the radular sac the two pedal ganglia are connected together by a wide short pedal commissure which passes from side to side below and in front of the posterior retractor muscles of the buccal mass, and behind and above them the terminal portion of the cephalic aorta passes downwards and backwards in the middle line. From this point the two ganglia pass downwards and backwards lying between the white muscle mass of the foot and the soft grey tissue of the sole. At first the two cords diverge somewhat, but posteriorly they again converge towards the middle line. A series of three or four transverse commissures pass across from side to side uniting them together at different points in their length. A series of nerves arise from the pedal ganglia and spread forwards and outwards. The first pedal nerve arises from just below the pedal commissure and passes forwards towards the anterior margin of the foot; it sends off a branch which passes inwards towards the middle line and forms an anastomosis with its fellow of the opposite side. The remaining nerves pass outwards in a radiating manner and form a very elaborate anastomosis around the margin of the foot. The nerves divide and anastomose in a series of loops and at certain points of the network so formed slight swellings can be detected, which probably correspond to local collections of ganglion cells. From the posterior surface of the pedal ganglia and the pleuro-pedal commissure several nerves pass backwards and enter the muscles of the foot. Each parietal ganglion gives rise to two nerves. The most anterior and smaller of the two is the mantle nerve, and the larger and more posterior is the parietal nerve. The two parietal nerves pass backwards and form a figure-of-eight loop in the visceral hump. Each nerve crosses over to the opposite side of the body from which it originated, and having done so sends off a lateral branch which anastomoses with the mantle nerve of that side, thus forming the ' dialyneural ' connection.

The right parietal nerve, or supra-intestinal nerve as it is called, passes obliquely across the upper aspect of the oesophagus just behind the buccal mass. In this portion of its course it is closely connected to, and surrounded by the branching follicles of the salivary glands. Having reached the left side it gives off a large branch, the anterior branchial nerve, which passes to the left and, having given off a small branch to join the mantle nerve, breaks up into a number of fine branches which supply the anterior region of the gill and the osphradium. At the point where the anterior branchial nerve arises from the supra-intestinal nerve a slight swelling is to be seen, this is known as the supra-intestinal ganglion. From this point the nerve passes up beneath the floor of the branchial chamber on the left side of the oesophagus. During this part of its course it gives off a series of fine branches to the gills and finally, at the extreme apex of the branchial cavity, a considerably larger branch, which soon subdivides into smaller twigs, is given off to the upper part of the gill.

The left parietal or sub-intestinal nerve crosses over from left to right below the oesophagus. It then diverges somewhat to the right and gives off a branch which again subdivides; one twig passes forwards and outwards to join the mantle nerve of the same side and the conjoined nerve so formed supplies branches to the outer wall of the syphon and the terminal portions of the excretory and genital ducts and the anus. The main nerve continues backwards above the columellar muscle at some distance from the oesophagus and gives off a series of branches to the mantle roof and its dependent structures. At the apex of the branchial chamber both nerves are continued up for a short distance in the floor and outer wall of the pericardium and then unite to form a loop, in front and to the inner side of the U-shaped bend of the oviduct in the ♀. At the apex of the nerve loop the nerve is slightly swollen and is known as the visceral ganglion. From it a series of branches arise which supply the neighbouring viscera.

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Part II.—THE EDGE OF THE MANTLE AND THE EXTERNAL ORNAMENTATION OF THE SHELL.

By N. Annandale.

In the first part of this paper Major Sewell has described the structure of the free part of the mantle of *Vivipara bengalensis* in general terms and has pointed out, as Leydig[1] observed in the embryo of *V. vivipara*, that the margin bears three short processes corresponding in position with the three rows of minute chaetae on the surface of the embryonic shell. He has further noted that in the adult additional processes are both intercalated between the three primary processes and produced to the left of the outermost row of chaetae in correlation with the development of dark spiral bands on the shell.

Similar facts struck me forcibly when examining two very large and peculiar species of Viviparidae in Manipur, namely *V. oxytropis* (Benson), the shell of which is ornamented with dark and prominent spiral ridges, and *Lecythoconcha lecythis* (Benson),[2] the shell of which is almost smooth and unicolorous.

The observations made on these species, supported as they were by Major Sewell's independent observations on *V. bengalensis*, led me to examine the edge of the mantle and the embryonic shell in all species of Viviparidae in which living or properly preserved material was available. The species I have examined living are *V. bengalensis* (Lamarck), *V. dissimilis* (Muller) [= *V. remossii* (Benson)], *V oxytropis* (Benson) and *L. lecythis* (Benson). I have also examined preserved material of the remarkable genera *Margarya*, Nevill, and *Taia*, Annandale, in both of which the shell is more highly and fantastically sculptured than in any species of *Vivipara*. My specimens of *Margarya melanoides* were collected in Yunnan by Mr. J. Coggin Brown, and those of *Taia intha*, *T. elitoralis*, *T. shanensis* and *T. naticoides* were preserved with great care by Dr. F. H. Gravely in the Southern Shan States. Some of them are in excellent condition for histological study.

In addition to this Asiatic material I have been enabled by the very kind assistance of Prof. J. H. Ashworth of Edinburgh University, to examine several series of fine sections of both the embryo and the adult of *V. contecta* (Millet), a European species with a smooth, broadly banded shell.

The material examined thus includes specimens and preparations of species both with smooth and with highly sculptured shells, both with almost unicolorous and with conspicuously banded shells.

[1] Leydig, *Zeits. f. wiss. Zool.* II, pl. xi, fig. 10 (1850).

[2] For the latter species I have recently proposed a new genus based partly on the structure of the mantle, viz. *Lecythoconcha*, Annandale, *Rec. Ind. Mus.* XIX. p. 114 (1920).

In considering the ornamentation of the shell both colour-pattern and sculpture can, therefore, be taken into account.

Ornamentation of the embryonic shell.

The ornamentation of the embryonic shell is almost uniform in pattern in all species of Viviparidae investigated, and the only important differences found are those in the degree to which the spiral sculpture is developed in different forms. Colour-pattern is usually absent, the shell being of a pale horny yellow or brown, with the protoconch darker and browner than the rest ; but in those species in which the embryo has a comparatively large number of whorls before birth the dark spiral bands characteristic of some such forms begin to appear on the younger parts of the shell before it is set free from the egg-membrane.

The sculpture at this early stage is mainly periostracal, involving only the horny outer covering of the shell ; but as this is not entirely so I propose to discuss the periostracal sculpture first and then that of the calcareous part of the shell or true test. It will be convenient to treat *V. bengalensis* as a typical form in discussing the periostracal sculpture of the embryo.

The shell of this species consists at birth of 3½ whorls. Of these the apical whorl and a half constitute the true protoconch. They are flat, band-like and almost smooth, but with a strongly marked keel running round the outer edge of their upper surface in a spiral. Several faint, line-like spiral ridges, of which two are more prominent than the others, can also be detected on their surface under a high magnification. A single spiral row of extremely fine hair-like processes projects from the marginal keel, extending upwards to the tip of the apical half-whorl. Towards the base of the protoconch these processes become stiffer and are curved and retroverted at the extremity, the curvature of their tips being directed towards the mouth of the shell. They also become less crowded together. A little above the point at which the protoconch merges into the uppermost whorl of the younger part of the embryonic shell (*i.e.* that part in which the whorls begin to assume the essential characters of those of the adult), a second line of chaetae makes its appearance parallel to the first, and finally, on the penultimate embryonic whorl, a third. The oldest row, which I shall call in reference to its age and its position the FIRST OR UPPERMOST ROW, is rather less developed than the SECOND OR MIDDLE ROW. The THIRD OR PERIPHERAL ROW, which continues to occupy the extreme periphery of the shell, is the largest and best developed of all. As the shell grows, however, and new whorls are added they destroy the chaetae that lie immediately above them by the pressure of their embrace.

Between the three primary rows of chaetae, above them to the left of the mouth of the shell, and particularly below them to the right (that is to say below the peripheral angle) there are other spiral lines on the external surface of the shell, running parallel to one another and to the rows of chaetae, but forming only very fine ridges with minute irregular processes or serrations. These I shall call the SECONDARY PERIOSTRACAL RIDGES of the embryonic shell. Finally, still finer oblique longitudinal or vertical lines can be detected under a powerful lens, running across the spiral lines in such a way as to form a delicate reticulation with rhomboidal meshes. That all this ornamentation is mainly periostracal can be proved by dissolving the calcareous matter of the shell with weak acid. The lines and chaetae remain intact.

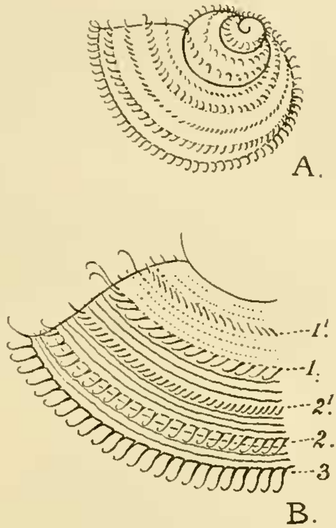

FIG. 10.—Embryonic shell of *Vivipara dissimilis* (Müller).

A. Oblique view of the whole shell at birth, showing lines of chaetae (magnified).

B. Part of the surface of the body-whorl of the same shell more highly magnified.

1 = uppermost primary row of chaetae;
2 = middle primary row of chaetae;
3 = peripheral row of chaetae;
1' 2' = secondary rows of chaetae.

In the other species of Viviparidae examined the periostracal ornamentation is essentially the same, but in several, the test-sculpture being more highly developed, the chaetae are given greater prominence. I will discuss this point later. In the embryonic shell of *V. dissimilis* (fig. 10), two of the secondary periostracal ridges bear minute chaetae considerably finer and shorter than those of the three primary rows but essentially similar in structure. These secondary rows are situated between the first and second primary rows and above the latter.

In some species the periostracal ornamentation of the embryonic shell becomes obsolescent at an early age, but in all I have examined the peripheral row of chaetae is continued, at any rate in some individuals, on to the body-whorl of the full-grown shell, and the apparent disappearance of the chaetae of the other rows is more apparent than real. These structures are of extreme fragility and in a comparatively heavy organism such as an adult *Vivipara* are liable to be rubbed off at a touch. In a nearly full-grown *V. bengalensis*, in which the shell is receiving its final addition, I have found that the three rows of chaetae are still produced, but disappear almost as soon as they are formed. In *V. dissimilis* traces of the embryonic periostracal sculpture are more persistent and the basis of the five rows of chaetae can frequently be detected in the form of fine punctures. Even in the adult of *L. lecythis* the periphery of the body-whorl is often surrounded by a line of extremely fine hairs representing degenerate chaetae. In the Siamese *V. ciliata* (Reeve),[1] in which a larger number of secondary periostracal ridges probably bear chaetae than in *V. dissimilis*, they persist throughout life on all the whorls of the shell, and in some individuals of the Chinese *V. lapillorum* (Heude)[2] they are coarsely developed on the peripheral keel of the body-whorl.

In species of *Vivipara* such as *V. bengalensis*, in which the embryonic shell is extremely thin and fragile, it is difficult to demonstrate the existence of any true test-sculpture as distinct from that of the periostracum, but by means of careful manipulation of lighting under a binocular microscope it can be seen that each of the rows of chaetae is situated on a slight elevation. This can be more readily demonstrated in such forms as *L. lecythis* (fig. 11), in which the test is much thicker at birth; while the chaetifer-

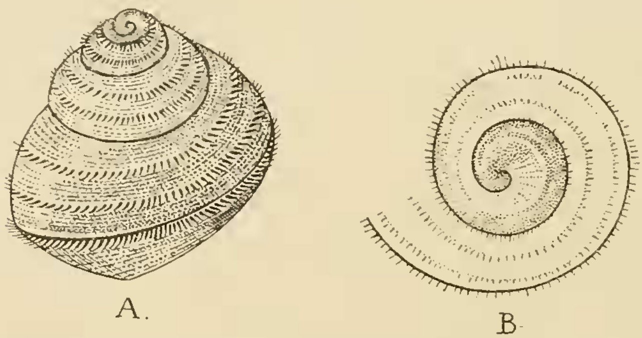

FIG. 11.—Embryonic shell of *Lecythoconcha lecythis* (Benson).
A. Lateral view of the whole shell at birth (magnified).
B. Protoconch as seen from above (more highly magnified).

ous ridges are conspicuous from the first in certain other species, such as *Margarya melanoides*,[3] *Taia intha*[4] and the peculiar Japanese *Heterogen turris*.[5] In these three species they are comparatively broad and blunt. In *V. dissimils* and *V. oxytropis*, although the embryonic shell is no thicker than in *V. bengalensis*, they are more prominent than in that species, but thin and sharp. Generally speaking, a strong development of the three primary ridges in the embryonic shell is correlated with a coarse and well-developed spiral sculpture in that of the adult, but this is not so in *Heterogen*, in which it becomes gradually much less conspicuous on the younger whorls. In *H. turris*, however, the only species of the genus known, as in the African *Neothauma*, Smith, and in many species

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[1] Reeve, *Conch. Icon.* XIV (*Paludina*), pl. vi, fig. 36 (1864).
[2] Annandale, *Mem. As. Soc. Bengal* VI, p. 314, pl. x, fig. 9 (1918).
[3] Kobelt on *Vivipara*, in new edit. of Mart. and Chemn., *Conch. Cab.*, pl. xxxvii, xxxviii (1909).
[4] Annandale, *Rec. Ind. Mus.* XIV, pl. xvii, fig. 7; pl. xviii, fig. 10 (1918).
[5] Annandale, *Mem. As. Soc. Bengal* VI, p. 400, figs. 1 2. (1921).

of *Vivipara*, the third or lowest primary ridge remains conspicuous as a peripheral carina, even when the other two disappear or become obsolescent.

Ornamentation of the adult shell.

In the adult shell, as I have already pointed out, the periostracal sculpture is relatively unimportant. In many species of the family, including the great majority of those of *Vivipara*, the test-sculpture is not much more conspicuous. In *V. bengalensis* the oblique longitudinal lines on the periostracum are impressed on the test and remain distinct through life. Indeed, they are coarser and more prominent in the younger whorls. In most races and phases of this species the spiral sculpture disappears almost completely on the body-whorl, but in some individuals of certain phases and races, such as the phase *halophila*, Kobelt (pl. II, figs. 9, 10), and the race *balteata*, Benson, the primary spiral ridges and also a few of those of the secondary order are slightly thickened on the body-whorl, while in the Burmese race (*doliaris*, Gould, pl. I, fig. 9) both the uppermost of the three primary ridges and the peripheral ridge are prominent, forming more or less sharp-cut angles in the outline of this whorl. In *V. oxytropis* and a few other species of the same genus the peripheral ridge forms a prominent keel on the body-whorl, separating the shell into an upper and a lower region, while some or all of the other ridges remain more or less salient.

It is, however, in such forms as the more highly developed species and varieties of the genera *Taia* and *Margarya* that the sculpture of the test reaches its highest development in the adult shell. In *V. oxytropis* [1] the ridges are smooth and sharp: in the more highly developed forms of the two genera mentioned they are broad and coarse and are broken up into numerous tubercles, scales or spines. Even in shells with a comparatively simple sculpture such as those of *Taia theobaldi* [2] or *Margarya melanoides* var. *mansuyi* [3] the ridges have not the unbroken surface of those on the shell of *V. oxytropis* and other ridged forms of *Vivipara*.

In all the Viviparidae in which I have examined both embryonic and adult shells, the ridges of the test are grooved internally at first. They retain this structure in *V. oxytropis* throughout life. In some other ridged species and races of *Vivipara*, however, with thicker shells, and also in all forms of *Taia* and *Margarya*, the internal groove becomes more or less completely obliterated by the deposit of nacreous matter on the internal surface.

In describing the ornamentation of the embryonic shell I have alluded briefly to the fact that in *Taia intha* and some other Vivi-

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[1] Hanley and Theobald, *Conch. Ind.*, pl. lxxvi, fig. 5 (1876).
[2] Annandale, *Rec. Ind. Mus.* XIV, pl. xvi, fig. 1 (1918).
[3] Kobelt on *Vivipara*, in Mart. and Chemn., *Conch. Cab.*, new edit., pl. xxxvii, figs. 6, 7 (1909).

paridae in which the shell attains a relatively large number of whorls before birth, a colour-pattern appears on the lower whorls, while in *V. bengalensis*, in which there are only 3½ whorls at birth, this pattern appears later. It cannot, therefore, be regarded as belonging to the primitive shell. Generally speaking, the shells of the Viviparidae may be divided into two categories so far as colour is concerned[1] The external surface in one category is of an almost uniform olivaceous colour, occasionally with irregular black longitudinal streaks. In the other type it is marked with dark spiral bands.

STRUCTURE OF THE MARGINAL REGION OF THE MANTLE.

By the phrase MARGINAL REGION OF THE MANTLE I mean the free edge of the roof of the branchial chamber and the immediately adjacent parts.

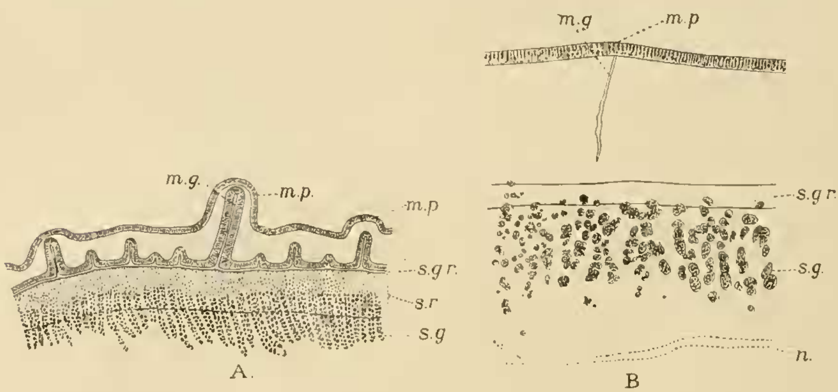

FIG. 12.—Edge of the mantle in *Vivipara bengalensis* (Lamarck), as seen by transmitted light (× 80).

A. In new-born young.

B. In half-grown individual at the end of a period of growth

m.g., marginal groove; *m.p.*, primary marginal process; *m.p.'*, secondary marginal process; *n*, nerve; *s.g.*, calciferous glands; *s. gr.*, supramarginal groove.

For the sake of brevity I shall refer to it merely as the marginal region. I do not propose to discuss the structure of other parts of the mantle except in so far as it may be necessary to elucidate that of this region.

EXTERNAL STRUCTURE.—The external structure of the marginal region is uniform in all the Viviparidae examined, so far at any rate as its main features are concerned, but exhibits certain minor generic and even specific characters, and differs in details at different periods in the life of the individual. The free edge is sharp at birth in *Vivipara* and *Taia*, blunt in *Lecythoconcha* and

[1] The only real exception I know to this rule is to be found in *V. helmandica* Annandale, from Eastern Persia, the shell of which is olivaceous with rounded pale spots, but there is often an obscure pale band round or just below the periphery of the body-whorl of the shell in forms of the *V. dissimilis* group.

also probably in *Margarya*, in which, however, I have examined only adult individuals. In the first three genera, and probably in all Viviparidae, it bears at this period three distinct finger-shaped processes,[1] one situated just above the snout near the middle of the edge, the other two to the right of this point. The left process, which marks a very important point in the orientation of the ornamentation of the shell, I shall call the PERIPHERAL PROCESS. It moves along, in the expansion of the animal, under the most prominent line of the body-whorl of the shell and is usually, but not always, a little longer than the others. The two processes to the right of the peripheral process may be called the first and the second process, the former lying the furthest to the right. These three processes correspond in position with the three primary rows of chaetae on the young shell (p. 250, fig. 13) and bear the same notation in my figures. The peripheral process, though usually the most conspicuous and the most important in the future history of the shell, is morphologically the youngest, while the first process, the least important of the three from this point of view, is the oldest. These three processes I call the three PRIMARY PROCESSES. They were first observed and figured in the embryo of *Vivipara vivipara* by Leydig,[2] but are omitted in the figures of more recent authors. I find them just as well developed in the fully formed embryo of the European *V. contecta* as they are in Indian species.

In most other Viviparidae examined, at least traces of other processes between and to the left of the primary three can be detected at the same period. In *V. bengalensis* (fig. 12) they are small and inconspicuous, but in *V. dissimilis*, another common Indian species, four SECONDARY PROCESSES can be easily detected in fresh material, two of them being longer than the other two. The two longest secondary processes are situated one immediately to the right of the second primary process and the other to the right of the third. They correspond in position with the two secondary rows of chaetae on the embryonic shell (p. 248, fig. 12). The condition is similar in *V. oxytropis*, but in *Lecythoconcha lecythis* only the three primary processes can be detected as such, even in fresh material.

Even the seven processes of *V. dissimilis* and *V. oxytropis* are not all that actually exist, for between each pair associated with lines of chaetae two or three other minute projections occur, but can only be detected as projections if the mantle be examined in a fully expanded condition. These minute or TERTIARY PROCESSES correspond in position with the minute serrated ridges on the periostracum of the embryonic shell (p. 245, fig. 10). Both they and the secondary processes are probably present and functional, though often difficult to detect, in all Viviparidae.

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[1] It may be fixed in this condition by being subjected to gentle pressure between two glass slides as soon as it is removed, and treated with corrosive acetic solution while under pressure.

[2] Leydig, *Zeits. f. wiss. Zool.* II, pl. xi, fig. 16 (1850).

The external structure of the processes (be they primary, secondary or tertiary) is identical. They are not mere projections of the margin but organs with a definite form, position and function. When fully expanded in the living animal they are flattened dorso-ventrally and sharply pointed, but it is difficult to preserve them quite in this condition as they usually become blunter and thicker in preservations, as they do in life when the mantle contracts (fig 12). Along the external surface of each, from a point close to the tip, runs a narrow groove, and the whole of both surfaces, including the floor of this groove, is densely covered with long and powerful cilia. These extend also all over the edge of the mantle. Very often (fig. 12) the presence of a tertiary, or even a secondary, process is only indicated by the existence of this groove, which I shall call a MARGINAL GROOVE.

The marginal grooves run up the external surface of each process to a broader and rather deeper transverse groove that traverses the whole of the margin just above the bases of the processes and

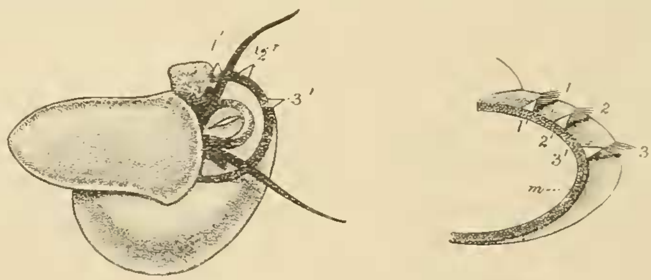

FIG. 13.—Living *Lecythoconcha lecythis* a fortnight old (magnified . *m.*, edge of mantle; 1, 2, 3, primary rows of chaetae on shell; 1,' 2,' 3', primary marginal grooves.

turns upwards for a short distance at the right extremity of the free edge. This groove I shall call the SUPRAMARGINAL GROOVE.

Immediately above the supramarginal groove on the external surface of the mantle is a broad and prominent ridge, which has been called the " white band " on account of its lack of epidermal pigment, but may be also known as the SUPRAMARGINAL RIDGE. Its surface is smooth and ciliated at birth in all the species examined at this period, and in *Lecythoconcha* its limits are not clearly indicated.

In the foregoing paragraphs I have described the external structure of the marginal region as it exists at the birth of the young mollusc, it remains to be seen how far it alters in the course of post-embryonic development. There is greater specific and generic variation in this respect than there is in the primitive structure, for while in some species and genera the marginal processes are greatly reduced in the adult, in others they retain their primitive condition, while in yet others they increase in proportionate development. I was under the impression that they disappeared completely in the adult of *V. dissimilis* and *L. lecythis*, so long as I examined only preserved material; but at any rate the three primary processes can be quite easily detected in the largest living individuals of the former species, while in full grown specimens of the *Lecythoconcha*, at least traces of the peripheral process sometimes persist and probably remain functional throughout life. In *L. lecythis* (fig. 13) the primary processes are very conspicuous for at least a fortnight after birth on account of their bright yellow colour as well as their prominence. Major Sewell (p. 220) has shown that even when the processes have apparently disappeared in *V. bengalensis* their position is apparently indicated by streaks of yellow pigment. In *V. oxytropis* both the primary and the secondary processes increase in actual size with the growth of the animal. In the living adult they are not so easily seen as the primary processes in the young of *Lecythoconcha*, because they are usually retroverted inside the shell when the animal is expanded, but even in material preserved by immersion in strong spirit and killed in a highly contracted condition, they can be detected without difficulty as soon as the shell is removed.

The fact seems to be, therefore, that these marginal processes are characteristic of the Viviparidae as a family. They differ in position and structure, and probably in function, from the processes present on the mantle of certain genera of Melaniidae,[1] and I have failed to trace them on that of any Hydrobiid. Their presence is, however, frequently concealed by contraction and shrinkage in preserved specimens, and the extent to which they actually degenerate or persist in the adult differs in different species.

Other questions that remain to be answered are those concerned with differences in the system of marginal and supramarginal grooves and in the supramarginal ridge at different periods in the life-history of the mollusc. What I have said of the marginal processes applies with equal force to the marginal grooves, except that in the adult of *Lecythoconcha* the peripheral marginal groove is sometimes still more distinct than the peripheral process, but in considering the subsequent history of the supramarginal groove another factor must be considered, viz. that of periods of growth and of rest. These affect the groove indirectly by affecting the ridge that lies immediately above it and can be discussed most conveniently when considering the internal structure of this ridge (p. 252). One point that may be noted here is that the cilia disappear from the surface of the ridge at an early period in post-embryonic life and that when the glands in it are in a state of activity its surface is minutely ridged at right angles to its own axis. Further, in growing specimens of *Taia intha*, preserved in a half-expanded state, the ridge bears cushion-shaped swellings opposite to, but much broader than, the primary processes.

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[1] See Benson, *Gleanings in Science* I, p. 21 (1830), and Annandale, *Rec. Ind. Mus.* XIX, p. 109 (1920).

It has not been necessary to say much about the edge of the mantle between the processes, the external structure of which offers no particular feature of interest at any time of life in most species. The difference between its conformation in *Vivipara* and *Taia* on the one hand and *Lecythoconcha* and *Margarya* on the other, already noted in the young (p. 249), is accentuated with the growth of the individual. It is, however, somewhat exaggerated in highly contracted or shrunken specimens. Another important generic difference, not following the same lines of division, may now be noted. It has a much more direct bearing on the special object of this section of our paper, as it is evidently correlated with the glyptic ornamentation of the shell. In *Vivipara* and *Lecythoconcha* the edge when fully expanded is straight, or rather curved in a wide arc outwards. It is, indeed, capable of considerable

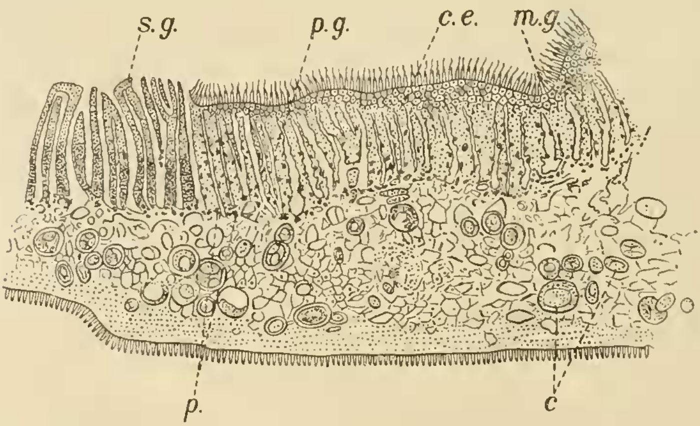

FIG. 14.—Horizontal transverse section through part of the edge of the mantle at the base of a primary marginal process of an adult *Vivipara oxytropis* (Benson), highly magnified and slightly diagrammatic.

c, calcareous concretions; *c.e.*, ciliated epithelium; *m.g.*, marginal groove of primary marginal process; *p.*, pigment granules; *p.g.*, periostracal glands; *s.g.*, calciferous glands.

change of shape and may become distinctly sinuate; but the irregularities of outline are mere irregularities without definite position or apparent function. This is also so in *L. lecythis*. It is unfortunate that I have not had an opportunity of examining either *Taia* or *Margarya* in a living condition in this connection, and in contracted specimens of these genera preserved in alcohol I can find no peculiarity of the edge of the mantle. In young examples of *Taia intha*, however, which were paralysed with menthol and fixed in 5% formalin without being fully contracted, a broad lobular projection can be detected at the base of the terminal scale-like projection on the peripheral ridge of the shell, proceeding for a short distance into the anterior cavity of the projection.

EPITHELIUM.—The epithelium of the extreme edge of the mantle is, as already stated, provided with long and powerful cilia. The cells are relatively deep and narrow and have large, deeply-staining nuclei. Unicellular glands do not occur among them. Epithelium of this type extends over both surfaces of the marginal processes and over the floors of the marginal and supramarginal grooves. Above the latter it gives place, but not abruptly, to non-ciliated epithelium containing unicellular glands. The change is gradual, the cells becoming shorter and stouter and the cilia more feeble and finally non-existent. On the surface of the supramarginal ridge, however, epithelium is usually absent after birth, the underlying glands being exposed on the surface.

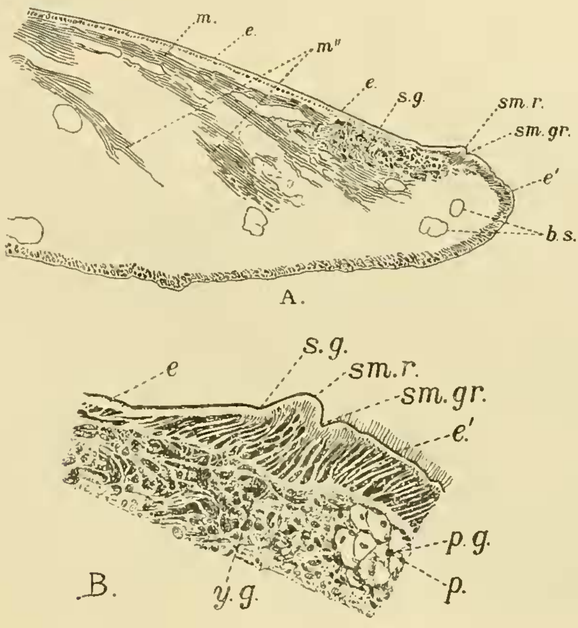

FIG. 15.—Vertical section through the edge of the mantle in the adult *Taia elitoralis*, Annandale, in a period of arrested growth.

A. The whole structure (× 80).

B. Region of the supramarginal groove more highly magnified.

b.s., blood-sinus; *e.*, non-ciliated epithelium; *e'.*, ciliated epithelium; *m.*, external retractor muscle; *m''.*, muscular network; *p.*, pigment granule; *p.g.*, part of periostracal gland; *s.g.*, degenerate remains of shell-gland; *sm. gr.*, supramarginal groove; *sm. r.*, supramarginal ridge; *y.g.*, yellow granules.

CONNECTIVE TISSUE.—Two kinds of connective tissue can be distinguished in the marginal region of the mantle of the Viviparidae. The bulk of the roof of the branchial chamber consists of a peculiar kind of cells closely resembling that of which the adipose fins of fishes are mainly composed and identical with those of the foot of the molluscs. These cells are of very large size and of polygonal outline (pl. iii, fig. 3). Their walls are thick, their nuclei very small and they are gorged with a gelatinous substance evidently not protoplasmic. Immediately under the epithelium of both surfaces of the mantle a thin layer of undifferentiated connective tissue can also be distinguished. It is thicker at some places than at others but has no particular feature of interest.

MUSCLES.—The muscular system of the mantle is complex in all genera of the family, but more so in some than in others. In *Vivipara* it is comparatively simple. In this genus a relatively thin sheet of longitudinal fibres extends down the external surface as far as or nearly as far as the upper limits of the supramarginal ridge. This may be called the EXTERNAL RETRACTOR OF THE MANTLE. In a corresponding position on the internal surface a few fibres of a similar nature can be distinguished, but they are poorly developed. In the neighbourhood of the supramarginal ridge a strand of oblique or nearly transverse fibres runs along parallel to

FIG. 16.—Microphotograph of vertical section through the edge of the mantle in *Margarya melanoides* var. *carinata*, Neumayr. The ciliated epithelium has been removed from the surface below the shell-glands.

b.s., blood-sinus; *e.*, epithelium; *m.*, external retractor muscle; *m'''*., muscular network; *s.g.*, calciferous gland; *y.g.*, yellow granules.

the margin rather deeper in the tissues and forms the SPHINCTER OF THE MANTLE. Its structure is simple in this genus and it is not powerfully developed. Finally, the external retractor sends numerous fine branches obliquely into the thickness of the mantle, in which they ramify and anastomose to form a loose MUSCULAR NETWORK.

In other genera the same elements of musculature are found, but variously developed. In *Taia* and *Margarya*, in which the sphincter is still more feebly developed, the muscular network is closer and has much smaller meshes and the individual strands are finer. In *Margarya*, in which the mantle is greatly thickened, it is better developed than in *Taia*.

It is, however, in *Lecythoconcha*, in which also the mantle is thick, that the muscles are the most powerful among the forms examined. The external retractor and its branches are both very coarse, but the latter are not numerous and the muscular network is not well developed. The sphincter, however, is both thick and complex, consisting of several strands which run obliquely in the midst of the shell-glands. Their position in reference to the edge of the mantle differs in different states of expansion and retraction (figs. 3, 4, pl. iii).

NERVES.—I have not attempted to work out the nervous system of the marginal region in detail and have not observed any external sensory organs. The whole of the roof of the branchial chamber is supplied by nerves arising from the parietal ganglia (Sewell, p. 240). In the marginal region a fairly stout transverse nerve can be readily distinguished, pursuing an irregular course above the supramarginal ridge, some parts of it being much nearer the margin than others. From it finer nerves run down at irregular intervals among the shell-glands. Their position is not definitely correlated with that of the marginal processes (fig. 12 B, p. 248).

VASCULAR SYSTEM.—The marginal region of the mantle is highly vascular in all species of Viviparidae examined. Definite blood-vessels can be seen entering it, but for the most part the blood is contained in irregular sinuses without definite walls. These reach their maximum development in the primary marginal processes of *Vivipara oxytropis* (pl. iii, fig. 5), in which the connective tissue has a strictly cavernous structure. A vascular system of this type cannot be investigated in detail without careful injection. This method I have not attempted to adopt as it is quite sufficient for my purpose to know that the processes, and indeed the whole of the edge of the mantle, are erectile rather than muscular, though their erectility is doubtless correlated with the action of the muscles of the roof of the branchial chamber.

SHELL-GLANDS.—A most important part of this investigation refers to the structure, position and function of the glands that secrete the substance of the external layers [1] of the shell and their relation to the external structure of the marginal region of the mantle and the ornamentation of the shell. The main facts about these glands have long been known and certain important points were made clear by Leydig,[2] Mer and Longe [3] and Moynier de Villepoix,[4] but I have failed to find in zoological literature any discussion of their comparative anatomy and functions in any one family of Gasteropods. As my own observations are in general agreement with those of the authors cited I will give an account of what I have myself seen without further historical discussion.

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[1] I do not propose to deal with those that secrete the internal nacreous layer.
[2] *Zeits. f. Wiss. Zool.* II, p. 123 (1850).
[3] *Comp. Rendus* XC, p. 882 (1880).
[4] *Comp. Rendus* CXIII, p. 317 (1891) and CXX, p. 512 (1895).

The glands (fig. 14, p. 252) concerned with shell-sculpture in the Viviparidae belong to two distinct series, differing in structure, position and function. We may call them respectively CALCIFEROUS and PERIOSTRACAL GLANDS in reference to the nature of their secretions.

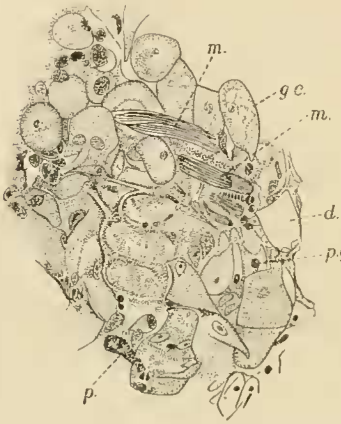

FIG. 17.—Vertical section through part of the periostracal gland in an adult *Vivipara contecta* (Millet) towards the end of a period of growth (× *ca.* 333).

d., duct of gland; *g.c.*, gland cell; *m.*, fibres of sphincter of the mantle; *p.*, suffused black pigment; *p.g.*, black pigment granule.

The periostracal glands are the smaller, less conspicuous and nearer to the free edge of the two series. They lie opposite the bases of the marginal processes and extend both upwards beneath the calciferous glands and downwards into the processes, at the base of which they open into the supramarginal groove by a series of very minute pores, one for each gland (pl. iii, fig. 1). In the young molluscs at birth each gland is a simple tubule formed of a single layer of gland-cells and more or less twisted in its course, which is tangential to the free edge and lies amidst the thick-walled cells of the interior of the marginal region. Later the glands become contorted and the cells proliferate to form an irregular mass (pl. iii, fig. 3). A definite duct is then developed, lined with very minute flat epithelial cells. It makes its way to the external pore from a small reservoir lying in the substance of the margin and also lined with minute flattened epithelial cells. Into this the secretion of the gland is evidently poured. The gland-cells (fig. 17) are relatively small and ovoid in outline. Their contents do not stain deeply except at birth and they become very inconspicuous in periods of arrested growth. In those species of Viviparidae that have dark-banded shells, such as *V. bengalensis*, *V. oxytropis*, *V. contecta*, and the young of *Taia intha* and *T. elitoralis*, very minute granules of black pigment are found in the cells and lining the ducts of the glands, but they are absent or very scarce in species with unicolorous shells, such as those of *V. dissimilis* and *L. lecythis*, except at the end of growth-periods, when dark pigment may become widely suffused among the interior cells of the mantle and is then by no means confined to the immediate vicinity of the periostracal glands.

The calciferous glands are larger, more numerous and more conspicuous, and occupy a higher and more superficial position on the mantle than the periostracal glands. They undergo, moreover, greater changes in the course of post-embryonic life and show a greater range of structural difference in different genera. I shall first describe them as they occur in the young of *Lecythoconcha lecythis* at birth, for they are greatly hypertrophied at the time in that species, occupying practically the whole of the external layer of the roof of the branchial chamber, lying immediately or almost

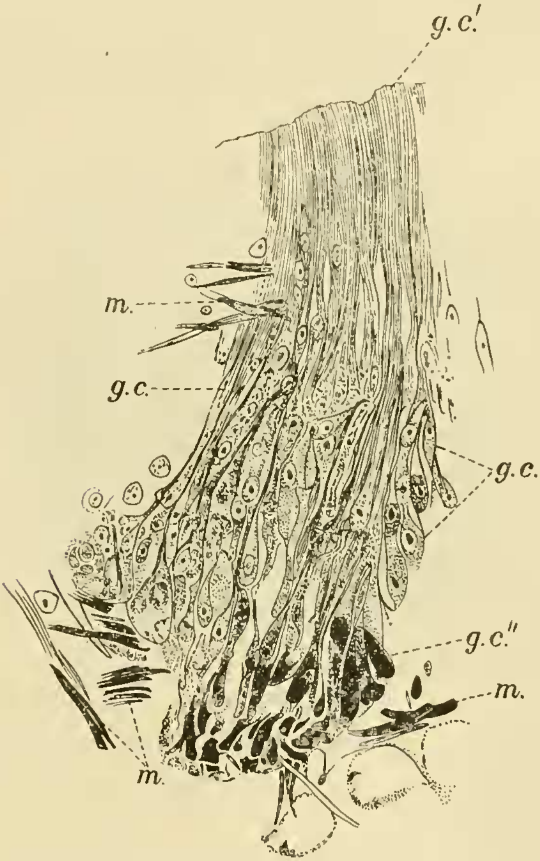

FIG. 18.—Vertical section (slightly oblique) through part of a calciferous gland of the same individual as figured in fig. 17 (same magnification).

g.c'., necks of gland-cells opening on the external surface of the mantle; *g.c''*., degenerating gland-cells. Lettering otherwise the same as in fig. 17.

immediately beneath the external epithelium and extending downwards into the substance of the mantle for nearly half its thickness.

In a vertical section of the mantle passing through the peripheral marginal process (pl. iii, figs. 1, 2) the tissues can thus be separated at sight under a low power of the microscope into an external glandular area and an internal vascular layer. It is with the former we are at present concerned. At the extreme margin, in the substance of the process, the periostracal glands can be distinguished, lying in the external part of the vascular layer. External to them, and not extending quite so far downwards or entering the process, the calciferous glands occupy the whole of the glandular area. These latter glands form in sections of the kind a series of minute tubules with their main axis at right angles to the surface, but a careful examination of a series of sections indicates that the tubules are not really separate but form a continuous or almost continuous tube with numerous closely adpressed loops. The uppermost loops are already degenerating and do not stain well aud those quite near the margin are not closely adpressed and have their cells smaller and probably not yet functional. In the upper part of the marginal region, however, the glands are well

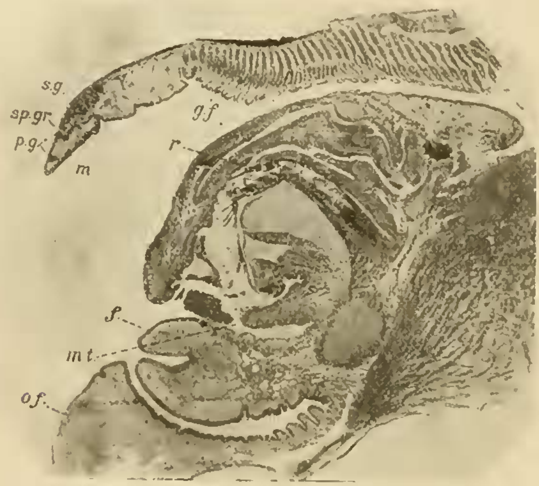

FIG. 19.—Microphotograph of a vertical section through the anterior part of the body of a young *Vivipara contecta* just before birth, to show general position of shell-glands.

g.f., gill-filaments; *f.*, foot; *m.*, mantle; *mt.*, mouth; *p.g.*, periostracal land; *gr.*, radula; *s.g.*, calciferous gland; *sp. gr.*, supramarginal groove; *o.f.*, operculiferous lobe of foot

developed and evidently functional. Here they consist of large deeply staining cells arranged in parallel rows from just below the external epithelium inwards to the base of the glandular layer.

In the young of other species (fig. 19) the structure of these glands is not essentially different, though they do not occupy nearly so large an area and are relatively much smaller. Their tubular conformation and the adpressed loops of the whole gland are just as well marked and the cells are similar in form and appearance.

At subsequent growth stages, however, a considerable change takes place. The cells are greatly reduced in numbers but increased in size and become ampulliform with extremely elongate "necks" and swollen proximal parts. The loops of the primitive gland, moreover are converted into groups of cells of the kind, each arranged round a small and ill-defined space. Their swollen proximal extremities lie buried in the mantle, while their necks extend outwards, closely pressed together, and reach the external surface.

In a vertical section they have in the mass a fibrous appearance which renders them liable to be mistaken for muscle fibres unless differential stains are used, and as the main axis of the cells is not quite at right angles to that of the surface, sections have to be slightly oblique to show their structure in detail.

The extent to which degeneration of the calciferous glands takes place in the rest-periods that succeed those of active growth differ in different species and probably in different circumstances, but they never completely disappear and even when completely degenerate form a conspicuous feature of sections of the marginal region of the mantle even under low powers of the microscope. Generally speaking, the degeneration appears to be greater in forms from a colder climate than it is in tropical species, probably because the alternate periods of growth and rest are more absolute in the former. Major Sewell's observations on the rate of growth in *Vivipara bengalensis* in Calcutta (p. 280) seem to show that growth may be, if not absolutely continuous, at any rate very readily revived at any time of year, whereas in *Taia intha*, which lives at an altitude of 3000 feet in a much colder climate, few shells were observed in early spring that appeared to be in a state of active growth. I find that the European *V. contecta* agrees with this species and its congener *V. elitoralis* from the same lake and also with *Margarya melanoides* (fig. 16, p. 254), which lives at greater altitudes in Western China, in having the glands very degenerate in periods of rest, whereas in *V. bengalensis*, *V. dissimilis*, *V. oxytropis* and *Lecythoconcha* it alters little in structure.

In those species in which the glands become most degenerate in periods of rest, as for example in *Taia elitoralis* (fig. 15, p. 253), the periostracal glands practically disappear, while the calciferous glands are reduced to an amorphous mass in which the cell-limits are distinguished with difficulty. This is most marked in their "necks," which fuse together to form a structureless or almost structureless layer on the external surface. When this occurs the flat epithelial cells of the upper part of this surface encroach to some extent on the area previously devoid of epithelium, while the ciliated columnar cells of the extreme margin apparently become more vigorous but do not extend upwards beyond the position of the supramarginal groove, which practically disappears as such. In preserved specimens in this condition I am unable to detect any trace of the marginal processes and grooves, but possibly they may be still present in the living animal.

The degeneration of the gland-cells is correlated with the secretion of certain yellowish granules of variable size and irregular shape, which are formed in them and finally become very conspicuous, even when the mantle is examined whole as a transparent object under a low power of the microscope (fig. 12, p. 248).

Refractile Bodies.—Throughout the vascular parts of the anatomy of the Viviparidae, and especially in the mantle, numerous small refractile bodies can be distinguished under a low power of the microscope. They are spherical or occasionally ellipsoidal in form and become more numerous in the half-grown and adult animal than they are in the young. Their size varies in different species and they are largest (among the forms examined) in *Lecythoconcha lecythis*. Unstained they are colourless, but they absorb stains such as haematoxylin and borax carmine readily and these stains, if the bodies are cut in sections, penetrate throughout their substance. They dissolve, however, immediately in acid and therefore disappear in a technique in which the use of free acid is involved, leaving open spaces that may easily be confused with small blood-sinuses. Their position is extracellular, but they occur in the peculiar gelatinous tissue described above. When the mollusc is in a state of active growth they congregate in large numbers between the shell-glands and the internal surface of the mantle (fig. 14). Externally they are perfectly smooth. Their internal structure is lamellar and concentric, but the lamellae of which they are composed are not numerous.

The structure of the shell-glands of both series is essentially similar in the Melaniid genera *Melanoides* and *Acrostoma* to that here described in the Viviparidae. As de Villepoix[1] has shown that it is also similar in *Helix*, we may assume that it is of a type widely distributed among the Gasteropod molluscs. It will therefore be worth while, before discussing the function of the glands and of the marginal region generally in relation to the ornamentation of the shell, to summarize the description already given so far as its main points are concerned. I have been able to find no detailed account of the external structure of this region, which probably differs greatly in different forms, in any other family. Even if certain features are peculiar to the Viviparidae, parallel, if not precisely analogous, features probably exist in other families.

Summary Account of the Ornamentation of the Shell.

The ornamentation of the shell in the Viviparidae is partly periostracal, partly impressed on the outer calcareous layers. In the embryonic shell, including the protoconch, both horny and testaceous structures are already concerned, but the periostracal ornamentation, when magnified proportionately, is the more conspicuous.

The periostracal ornamentation is, at any rate in some species, both glyptic and coloured. Its sculpture is minute and consists of spiral rows of horny chaetae, fine spiral ridges and still finer oblique longitudinal lines. These are best developed in the fully-formed embryo and as a rule disappear or become obsolete (with the exception of the longitudinal lines, which tend to become more

[1] de Villepoix, *Comptes Rendus* CXX, p. 512 (1895).

prominent) in the full-grown shell. Three primary rows of periostracal chaetae can be distinguished, the best developed of which runs round the periphery of the whorls, while the other two are situated above it. The peripheral row, though the most important of the three, is the latest to be formed and only the first or uppermost row extends to the apex of the protoconch. In some species (e.g. *Vivipara dissimilis*), two additional rows of chaetae are present on the embryonic shell, one between the peripheral and middle row and one above the first row. These chaetae are, however, smaller than those of the three primary rows. They are homologous with two of the fine spiral ridges on the shells of other species.

In those species in which the shells are ornamented with bands of dark pigment the colour-pattern is periostracal in origin, though the calcareous matter may be slightly stained. The bands correspond in position with the rows of chaetae and spiral ridges.

The test-sculpture (*i.e.* that of the outer calcareous layers of the shell) also corresponds in position with that of the periostracum. In shells of the family in which it is highly developed, it consists mainly of prominent spiral ridges. These ridges may be smooth and uninterrupted (as in *Lecythoconcha lecythis*) or broken up more or less distinctly into series of tubercles (as in some individuals of *Taia naticoides*), scale-like projections (as in the most highly developed shells of *Taia* and *Margarya*) or even spines, as in the fossil *Rivularioides.*[1] They may be hollow as in *V. oxytropis* or solid as in the Chinese *V. lapillorum.* In practically all shells of all types the most prominent and most highly developed ridge corresponds with the peripheral row of chaetae, and in a large proportion those that correspond with the two other primary rows of chaetae are better developed than any others. Moreover, each ridge corresponds either with one of the primary rows of chaetae or with a secondary ridge of the periostracum.

SUMMARY ACCOUNT OF THE STRUCTURE OF THE EDGE OF THE MANTLE.

We may summarize the structure of the distal part of the mantle in the Viviparidae as follows:—

The free edge of the mantle is membranous, but much thicker in some genera (e.g. *Lecythoconcha*) than in others. The margin bears at least three digitiform processes, which are better developed in some species (e.g. *Vivipara oxytropis*) than in others, and are usually obscured by contraction and shrinkage in preserved material. In addition to those three primary processes other, smaller processes are present, probably in all cases, but are still more difficult to detect except in the living animal and may perhaps become vestigial in the adult of certain species. These primary and secondary processes correspond in position with the

[1] Annandale, *Rec. Geol. Surv. Ind.* L, pl. xxxiii, figs. 7–12 (1919).

periostracal sculpture. Immediately above the processes a groove runs transversely across the external surface and from it short longitudinal grooves are given off at right angles and run to the tip of the processes. Above the transverse supramarginal groove and running parallel to it, a convex ridge, varying in breadth and prominence at different stages of growth, can usually be traced. For it I have proposed the name of supramarginal ridge. The margin, including the grooves, is covered with columnar ciliated epithelium as far up on the external surface as the lower edge of the supramarginal ridge. Except at a very early stage in free life (*Lecythoconcha*) the epithelium is degenerate on the ridge, and above it consists of non-ciliate cells.

The substance of this part of the mantle is composed mainly of a peculiar kind of connective tissue consisting of polygonal cells with small nuclei, rather thick walls and gelatinous contents, in the main non-protoplasmic. It is cavernous in structure, including numerous ill-defined blood-spaces without cellular walls as well as true blood-vessels. Longitudinal muscles, sometimes powerfully developed, run down the mantle under the external epithelium, and certain oblique strands can also be followed out near the margin, forming a sphincter round the aperture of the branchial chamber. A fine network of muscle fibres also extends inwards from the outer layer. The musculature is much more highly developed in some genera than in others.

The nervous system of the margin has not been worked out in detail, but an irregular transverse nerve, some parts of which are nearer the edge than others, runs above the supramarginal ridge, and sends down fine longitudinal strands at intervals to the calciferous glands.

The glands whereby the greater part of the substance of the shell is secreted lie just above the edge of the mantle and are of two orders, the periostracal glands, which secrete the periostracum or epidermis of the shell, and the calciferous glands, which secrete the calcareous matter. The former are true multicellular glands of a vermiform shape, consisting of contorted tubules and opening to the surface by ducts with cellular walls. They lie some distance below the external surface in a transverse series along the extreme margin, for the most part beneath (*i.e.* distad of) the calciferous glands and with the main axis of each gland at right angles to the margin. Their ducts open into the supramarginal groove. The calciferous glands are much more bulky and differ considerably in structure. They occupy the supramarginal ridge and as a rule extend slightly beyond it both above and below, lying only a short distance beneath, or actually on, the surface and having no cellular ducts. Like the periostracal glands they form a transverse series, though the main axis of each gland is at right angles to the margin. Each gland is at first an elongate cylindrical tubule of gland-cells forming a large number of closely adpressed loops in the external margin of the connecting tissue. The cells are large and do not appear to have any very intimate organic connection *inter se.* The lumen of the tubule has no special lining. At this stage ducts, perhaps of a temporary nature, can be detected in sections, but they form mere gaps in the epithelium, leading out from ill-defined spaces beneath it (fig. 2, pl. iii). Later the gland-çells become greatly enlarged and elongate and open direct on the external surface; while the tubular character of the gland disappears.

The calcareous matter secreted by the calciferous glands is apparently derived from concretions scattered through the connective tissue of the mantle and foot but congregated in large numbers immediately beneath the glands at times of active growth.

The secretion of the nacreous layers, probably affected by unicellular glands scattered over the whole of the upper part of the mantle, is not discussed here.

Function of the different parts of the Marginal Region in reference to the Shell.

We are now in a position to discuss the function of the edge of the mantle in relation to the ornamentation of the shell. The first structures in the soft parts to be considered in this connection are the marginal processes. They are not organs of secretion but, at any rate when hypertrophied as in *V. oxytropis*, perhaps accessory breathing organs. They are closely correlated in position with both the periostracal sculpture, the colour-pattern and the sculpture of the test. The connection between them and the periostracal sculpture can be traced without difficulty. They mould this sculpture, apparently as erectile rather than muscular organs. The horny matter that will form the thin outer cuticle of the shell is poured in a liquid condition into the supramarginal groove, in which it is kept in motion by the cilia of the epidermal cells. It runs down the longitudinal grooves on the external surface of the processes and by them is deposited on the edge of the lip of the shell, over which they are retroverted as it consolidates. The three primary rows of chaetae are thus formed by the three primary processes, and in such forms as *Vivipara dissimilis* in which there are more than three rows, those of the secondary rows by the best developed of the secondary processes. The upright form of the chaetae is due to the greater length of these processes. This enables them to project well beyond the lip and be curled up over it. The hooked tips of the chaetae are due to the fact that the tips of the processes are curved at the moment of formation of the chaetae. The fine subsidiary ridges of the periostracum, which when first formed project horizontally from the edge of the lip as fine hairs, are similarly produced by the subsidiary processes, their orientation being due to the fact that the moulding processes are short and cannot be curved upwards over the lip.

In those shells which like *Vivipara bengalensis* have a pattern of dark spiral bands in the periostracum, the dark pigment is also poured out along the grooves on the external surface of the marginal processes. This is proved not only by the position of the bands and their arrangement on the shell but also by the close correlation of dark pigment with the periostracal glands in such species and by its absence from the margin in those species the shells of which are not marked with dark spiral bands. We may presume that, after the secretion of the horny fluid to form the chaetae and ridges, the pigment is poured out in a similar manner along the processes and deposited by them on the surface of the lip. The chaetae themselves are not coloured by it, and I do not think that the ridges are either, though this point is difficult to observe with certainty, because the dark bands do not appear until the shell has become fairly opaque and the ridges project very little from the surface.

To return to the periostracal sculpture, the fine vertical lines are evidently due to a pouring out of horny matter direct from the supramarginal groove, with which they correspond exactly in orientation, each representing, so to speak, a separate act of secretion.

The sculpture of the test also corresponds closely in position and arrangement with that of the periostracum and, indeed, so far as the minute sculpture is concerned, is practically a cast of it from which the upright chaetae are necessarily omitted, just as single upright hairs cannot be represented in a plaster cast. In most forms of *Vivipara bengalensis*, and indeed in most Viviparidae, there is nothing more to be said on this point, but in those species which have highly sculptured shells, and even in some phases and individuals of *V. bengalensis*, a further exposition is necessary.

The highly sculptured shells among the Viviparidae fall into three categories, viz. (1) very thin shells with uninterrupted, *hollow* spiral ridges; (2) thicker shells with uninterrupted, *solid* or almost solid spiral ridges, and (3) shells, thick or thin, with ridges that are more or less distinctly broken up into nodules, scales or spines.

Of the first type, which is the scarcest of the three, *V. oxytropis* is an excellent example. The shell, in spite of its large size, is exceptionally thin and fragile and the ridges upon it though prominent are very little thicker than the intervening spaces on account of the well-marked concavity of their internal surface, which forms a regular groove. No peculiarity of the calciferous glands has been observed in connection with these ridges on the shell, and none is necessary to explain them, for they lodge the greatly hypertrophied marginal processes, the mere presence of which on the internal surface of the shell while the calcareous matter was soft is sufficient to account for their presence.

On shells of the second type with solid uninterrupted ridges no satisfactory direct observations have been possible, owing to imperfect preservation of the material available, but the marginal processes are not hypertrophied as in *V. oxytropis* and it may perhaps be assumed that the ridges are due to a certain slight hypertrophy of the calciferous gland in a position on the mantle corresponding with them on the shell. This is indicated by the facts that even in smooth shells of *V. bengalensis* the dark spiral bands are slightly thickened and that at the end of a growth-period the calciferous glands are often a little larger immediately above the primary marginal processes than at other points on the periphery. It is clear, however, that some of the matter which occupies their base is nacreous, and we know that on the internal surface of the shell nacre can be deposited by almost any part of the mantle after the external ornamentation is complete.

The third, most highly sculptured type of shell is the most interesting of the three, not only because of its peculiar facies but also because it has appeared and become dominant among the Viviparidae[1] on different occasions and in different places and different geological epochs. The test sculpture, even in this type of shell, corresponds closely in fundamental pattern with the primitive periostracal sculpture of the embryo of *V. bengalensis*, that is to say that it consists essentially of spiral ridges bearing prominences and that these ridges have fundamentally a definite number and position on the shell exactly similar to that of the three rows of chaetae and the secondary ridges of the embryonic periostracum, and that the most prominent ridge corresponds with the peripheral row of chaetae. It follows that the interrupted ridges of the test in this type of Viviparid shell are correlated at least in position with the marginal processes of the mantle, but the connections between the structures on the shell and those on the soft part are certainly not so close as in the periostracal sculpture and cannot be stated with the same precision. Here again, however, we know that the test sculpture is not correlated as in *V. oxytropis* with any hypertrophy of the marginal processes of the mantle, which are small in both *Taia* and *Margarya*, and also that the processes show no essential difference of structure in individual shells of the former genus in which the sculpture is less and more highly developed.

If the mode of construction of the projections on the peripheral and other ridges of the more highly developed shells of the genera *Taia* and *Margarya* can be explained, that of the remainder of the ridges is a simple matter. They cannot have been formed, so to speak, in the air (or rather in the water) but must have been built up in continuity with the edge of the lip. In the fossil *Rivularioides* they may be nearly half as long as the diameter of the whole shell. Their form suggests that they must have been moulded by some comparatively broad projection of the mantle edge. In contracted specimens of *Taia* and *Margarya* no trace of any such structure can be detected, and the extreme margin differs little from that of *V. dissimilis*, which has a very smooth shell. It is unfortunate that I made no observa-

[1] Annandale, *Rec. Geol. Surv. Ind.* L, *p.* 209, pl. xxxi, figs. 8–11 (1919).

tions on the living *Taia* that would have thrown any light on this point, but I have been able to examine some well-preserved specimens of *T. intha* in which the animal is partially expanded and the mantle not completely retracted. In those in which the growth-period was completed when they were killed I can find no peculiarity in the margin of the mantle, which is either quite smooth or undulates gently, but in several specimens in which the extreme thinness of the lip proves that growth was still in progress, the base of the youngest scale-like projection of the peripheral ridge is still hollow and contains a broad lobe of the mantle-edge, evidently temporary in nature.

The projections on the shell, however, are not only of considerable length when highly developed, but contain a relatively large amount of calcareous matter. In both *Taia* and *Margarya* the calciferous glands degenerate greatly in the periods of rest and in full-grown individuals become very uniform all along the edge of the mantle, but in a young growing specimen of the *Taia intha* I find that immediately opposite the peripheral ridge there is a cushion-like thickening of the supramarginal ridge due to the greater depth of the glands at this point. In the individual in which this observation was made a scale-like projection was in the process of formation. In others, in which this was not so, the glands at the same point were not hypertrophied to any appreciable degree.

It follows, therefore, that the projections are formed owing to periodical hypertrophy of the calciferous glands in the part of the mantle that lies immediately beneath the ridge on the shell, and moulded into shape by temporary lobes of the mantle edge. The difference between the smooth ridges on the shell of such species as *Vivipara lapillorum* and the interrupted ridges, often with relatively long projections, of such forms as *Taia intha* or the var. *carinata* of *Margarya melanoides* is probably, therefore, due to the local hypertrophy of the calciferous glands being in one type of shell permanent, and in the other temporary. Elongate projections on the ridges of the most highly sculptured shells of the family are secreted thus and are modelled into shape by the temporary lobes. It is noteworthy that whereas the muscles are not so coarse, and the transverse fibres distinctly less well-developed, in the marginal region of the mantles of *Taia* and *Margarya* than in the smooth-shelled *Lecythoconcha lecythis*, the two former genera have a regular network of muscles pervading almost the whole mantle in a manner not observable in *L. lecythis* or any other species of the family examined. This may doubtless assist in the projection of temporary lobes from the edge of the mantle.

The secretion of the periostracal glands probably mixes to some extent with that of the calciferous glands and forms the organic basis of the shell.

The dark margin of the mouth of the shell to be noticed in many species of *Vivipara* when the growth-period is complete is probably due to a general suffusion of black pigment correlated with its accumulation in the tissues at such periods.

Part III.—SYSTEMATIC.

By N. Annandale.

The smooth-shelled dark-banded Viviparae of India and Burma have given difficulty to all conchologists who have discussed them in a comprehensive spirit. This is because the shells are both variable individually and plastic in relation to environment. Local races are also liable to become differentiated, and we find a number of forms that appear at first sight to be specifically distinct but are actually linked together, as becomes evident where a sufficient number of specimens are examined, by innumerable intermediate types. Nevill in his unfinished *Catalogue of Mollusca in the Indian Museum* (1877), of which the only fragment published dealt with the Ampullaridae and Viviparidae, and in his later but also unfinished *Hand List of Mollusca in the Indian Museum* (1885), included most of those forms, with several others, as varieties and subvarieties under the name *Paludina bengalensis*. So far as the species found in India proper are concerned, I believe that his judgment was in the main just, but the forms he assigned in 1885 to *cingulata* (from Assam) and *polygramona*, von Martens, I regard as specifically distinct.

Under the specific name *Vivipara bengalensis* I include all the Indian forms of the genus with dark-banded shells, except the Viviparae oxytropides, undescribed species from Manipur and Preston's *Vivipara nagaensis*, the last of which I have not seen. Of *V. bengalensis* I recognise the following forms :—

Race *bengalensis* (Lamarck).
Race *mandiensis*, Kobelt.
Race *nepalensis*, Kobelt.
Race *balteata* (Benson).
Race *doliaris* (Gould).
Race *eburnea*, nov.
Race *colairensis*, nov.
Phase *annandalei*, Kobelt.
Phase *halophila*, Kobelt.
Phase *incrassata*, nov.
Phase *pachydolicha*, Annandale.

Vivipara bengalensis (Lamarck).

1822. *Paludina bengalensis*, Lamarck, *Anim. s. Vert.* VI (2), p. 174.
1920. *Vivipara bengalensis*, Annandale, *Rec. Ind. Mus.* XIX, p. 113.

The shell is ovate as a whole, sharply acuminate and with a relatively large subcircular or almost rhomboidal mouth, which is never very oblique. The upper part of the shell is slightly conoidal rather than strictly conical. There are $5\frac{1}{2}$ to $6\frac{1}{2}$ whorls, the suture is narrowly impressed and the whorls are somewhat but never very greatly swollen. The spire is relatively large, usually a little shorter than, but occasionally longer than the body-whorl. Its whorls increase in size evenly and gradually. The body-whorl is slightly oblique and always considerably broader than high, as seen in dorsal view. In this view it expands but slightly towards the outer margin. The umbilicus is narrowly perforate or completely closed, rarely more open, the columella is strongly arched, with a narrow margin and by no means prominent, the outer lip is almost semicircular, sharp, thin and joined to the columellar margin above as a rule merely by a thin, glary deposit. In the adult shell the sculpture consists of fine longitudinal ridges, which are convex outwards and on the body-whorl sometimes take the form of fine irregular ribs or varices. Only traces of spiral sculpture can as a rule be distinguished on adult shells, but the young shell bears rows of very fine punctae, representing the bases of minute chaetae. The colouration varies considerably, but is always some shade of greenish-olivaceous, marked with dark spiral bands. These are as a rule narrow, but broader bands alternate with still narrower, often paler linear ones of the nature of 'shadow stripes.' The bands are occasionally rendered obsolescent, though rarely or never quite obsolete, either by a general deposit of dark pigment or by an incomplete albinism. The fully developed mouth usually has a narrow black rim.

The operculum is moderately thin and of a deep brownish colour. The external surface is concave as a whole. The outer margin is strongly curved, the inner margin slightly sinuate and the posterior extremity bluntly pointed. The muscular scar is moderately large and prominent, much deeper in colour than the rest of the operculum.

In all races two types of shell can be found. They may be called the normal type and the elongate. In the former the shell is considerably more globose, broader in proportion to its height, with a larger mouth and a shorter spire than in the other. The difference is not sexual, but apparently dimorphic. In most races the normal type is much the commoner, but in the phase *annandalei* the proportionate numbers of the two are reversed, and this is also so in the race *baltcata*. In the race *colairensis* the normal type is about as elongate as the elongate type in the *forma typica*, but shells of a still more elongate type are also found occasionally.

In the *forma typica* and in the race *mandiensis* a third type of shell is sometimes found. It may be called the gigantic type, for its characters are great size, more swollen whorls, broader umbilicus and more projecting mouth. Sometimes, especially in large marshes, this type shows a tendency to predominate and almost assumes the rank of a phase.

Yet a fourth type occurs, much more rarely than the others, namely, the canaliculate, in which the outline is extremely broad and the surface outside the suture deeply impressed. Single shells of this type have been found in the *forma typica* and in the dark form of the race *eburnea*.

The elongate type of shell was called *Paludina elongata* by Swainson, the gigantic *P. gigantica* by Reeve and the canaliculate *P. bengalensis* var. *canaliculata* by Nevill, but I have avoided the use of these latinized names, for as a rule they apparently represent mere aberrations.

Soft parts.—As yet we know too little about the details of the comparative anatomy of the Viviparidae to say with certainty what characters in the soft parts are of specific importance, but the following four points may be noted wherein a definite anatomical difference exists between *V. vivipara* and other species for which information is available :—

1. The marginal processes of the mouth are moderately well developed, less so than in *V. oxytropis*, but more so than in the adult of *V. dissimilis* and *V. vivipara.* Three are much larger than the others.

2. The testis consists of a single lobe, not of two subequal lobes as in *V. vivipara* or of a large primary lobe with an ill-developed second lobe as in *V. dissimilis.*

3. The male tentacle is less differentiated than in *V. vivipara,* but not less so than in *V. dissimilis* and other Indian species examined.

4. The right pleural ganglion is almost completely fused with the right cerebral ganglion, whereas in *V. vivipara* there is a short but distinct commissure.

Radula.—The radula is chiefly noteworthy for the following points :—

1. The teeth are moderately large and stout and have their denticulation well but not immoderately prominent.

2. The central is relatively large and considerably broader than long. Its distal margin is distinctly concave. The lobe in the middle of its cutting edge is quadrate, much broader than deep and relatively large. It has on each side of it at least five triangular denticulations ; which are sharply pointed and decrease in size gradually from within outwards.

3. The two laterals and the marginal on each side are relatively broad and not very much longer than the central. Their denticulations are comparatively coarse and on the laterals closely resemble those on the central. On the marginal they are much finer and there are over twenty. The upper extremity of the edge of this tooth is usually expanded to form a small triangular process.

The foregoing description and observations are intended to apply to the species as a whole. I will describe separately the various races that occur in different parts of the Indian Empire, and then the phases, whose peculiarities are probably due to some physical factor in their environment acting directly on the individual, rather than to geographical isolation of the race.

The anatomy of the Viviparidae, so far as it has been studied, is strikingly uniform in most respects and little or no recognisable difference has been found in the different forms of *V. bengalensis* so far as the radulae and soft parts are concerned. In the radular teeth slight racial peculiarities might perhaps be found, but they are so ill marked that it would be misleading to lay stress upon them.

The different local races of *V. bengalensis* have the following distribution. The *forma typica* is peculiar to the lower Ganges valley. Westwards it is replaced, apparently quite gradually, by *mandiensis* and southwards by *eburnea*. The race *nepalensis* occupies the base and lower valleys of the Eastern Himalayas from Nepal to the east of Assam, but in the plains of Assam is gradually replaced by *balteata*, which in its turn gives way to *doliaris* in the valleys of Burma. In no instance is it possible to draw a precise line, either structural or geographical, between the different races.

The form that I have called race *colairensis* differs from the others here recognised as races, in that it has been found only in one locality. A large number of individuals were, however, examined and the racial characters seem to be remarkably distinct.

In a sense two (*incrassata* and *pachydolicha*) of the four phases here recognised, are modifications of the local race *eburnea* rather than of the species as a whole, but in the other two (*annandalei* and *halophila*) the phase-characters mask the racial ones and the phase is found in the territory of more than one race.

For these reasons I have carefully avoided a specious appearance of precision in defining the diagnostic characters of races and phases. I have also refrained from giving measurements of individual shells. These I have found most misleading in diagnosis, the differences in form depending not so much on point to point measurements as on the curvature and inclination of the outlines. Such differences can be properly demonstrated only by good figures. Unless it is otherwise stated, I have examined large numbers of specimens of each race and phase from several or many localities.

Race **bengalensis** (Lamarck).

(Plate 1, figs. 1–3.)

1822. *Paludina bengalensis*, Lamarck, *Anim. s. Vert.* VI (2), p. 174.
1822. *Paludina elongata*, Swainson, *Zool. Ill.* Ser. I, II, pl. xcviii top.
1841. *Paludina bengalensis*, Delessert, *Rec. de Coquilles*, pl. 31, figs 2a, 2b.
1852. *Paludina bengalensis*, Küster, in Martin and Chemnitz's *Conch. Cab., Paludina* I, p. 17, pl. 3, figs. 15, 16.
1862. *Paludina bengalensis* and *P. gigantea*, Reeve, *Con. Icon.*, pl. ii, figs. 5*a*, 5*b*, and 7.
1876. *Paludina bengalensis*, and *P. bengalensis* var. *gigantea*, Hanley and Theobald, *Con. Indica*, pl. lxxvi, figs. 8, 9, 10 and pl. lxxvii, fig. 5.
1877. *Paludina bengalensis*, (Typical sect. in part) Nevill, *Cat. Moll. Ind. Mus.*, pp. 26–28.
1885. *Paludina bengalensis* (in part), with subvar. *phaeostoma*, *elongata*, *gigantea* and *canaliculata*, Nevill, *Hand List Moll. Ind. Mus.*, II, pp. 20, 21.
1909. *Vivipara bengalensis*, Kobelt, in Martin and Chemnitz's, *Conch. Cab., Paludina*, II, p. 271, pl. lv, figs. 1–4.

I regard the race found in the lower Ganges valley as the *forma typica* of the species. The typical shell of this race is about $1\frac{2}{3}$ times as high as broad and the spire and body-whorl as seen in dorsal view are about equally high. The whorls are rather tumid and the body-whorl is evenly convex in profile, not biangulate. The mouth of the shell is sub-circular and has a narrow black margin when complete. It is nearly as high as the spire and very little oblique. The umbilicus is narrow. The colouration is never very brilliant. The ground colour is greenish and opaque. The dark bands are variable and irregular, but the alternating of broad and narrow bands can always be seen if the shell is clean. The bands are hardly incrassated. The interior of the shell is white.

The elongate type of shell occurs occasionally with the typical one. In it the height is about $1\frac{1}{2}$ times the maximum diameter. Its mouth is relatively small. The gigantic type is rarer than the elongate one, but occasionally occurs almost as a distinct phase. It is, however, also found with the typical form, apparently as an aberration.

Nevill has given the name subvar. *canaliculata* to a curious shell from Raniganj in Bengal. This specimen, which is the only one of the kind I have seen in this race, has a somewhat turbinate form and a broad, deeply impressed suture. It must be regarded as a mere abnormality.

This race is usually found in large ponds, marshes and backwaters with a properly aquatic vegetation. Where the vegetation is scanty the shells are usually dwarfed.

Race **mandiensis**, Kobelt.

(Plate I, figs. 4 and 10.)

1909. *Vivipara bengalensis*, var. *mandiensis*, Kobelt. *op. cit.*, p. 414, pl. lxxvii, figs. 8, 9.

This race is so like the *forma typica* that I have kept it distinct with some hesitation and only after ascertaining that the differences persist with fair constancy over a large territory. These differences, small as they are, are well shown on plate I. The spire is rather more conical and a little narrower than in the *forma typica*, the aperture not quite so broad, but more projecting, the umbilicus broader. There is great variation in colour, probably due to the nature of the water in which the animal lives. The shells in the type-series are pale, but have the alternating broad and narrow spiral bands well developed. Shells from Ambala in the plains of the Punjab are very similar. Specimens from shallow ponds in Lahore have the shell pale and translucent like opal glass, the periostracum extremely thin and evanescent and the dark markings often almost obsolete. In such specimens the animal is also very pale. Shells from the island of Bombay, on the other hand, are unusually brilliant in colouration, the ground-colour being bright olive-green and the bands well defined, dark and regular.

Type-series. No. M5081/1 *Z.S.I.*

Geographical range.—The type-series is said to be from Mandi, a small native state high up in the Kangra valley in the Western

Himalayas, but the fauna of this district is mainly Palæarctic and the occurrence of *V. bengalensis* needs confirmation. The specimens examined by Kobelt, moreover, agree precisely with those from the plains of the northern Punjab. The range of the race certainly extends from Allahabad at the junction of the Jumna with the Ganges to the northern limits of the plains of the Punjab on the one hand and to the shores of the Arabian Sea at Bombay on the other. It may be described as the common race of north-western India.

Both the "elongate" and the "gigantic" type of shell occur in this race occasionally, but the "normal" type is very much more common than either.

I have found this race in the Punjab in small ponds that in winter were extremely shallow and completely devoid of phanerogamic vegetation. In such environment the mollusc buries itself in the mud as the water dries up.

Race **nepalensis**, Kobelt.

(Plate I, fig. 7.)

1909. *Vivipara bengalensis*, var. *nepalensis*, Kobelt, *op. cit.*, p. 44, pl. xxlvii, fig. 10.

This race is rather more distinct from the *forma typica* than the preceding one, but many shells occur that would be difficult to assign to one race or the other and as a whole *nepalensis* merges so gradually into the still more distinct Assamese form *balteata* that it is impossible to draw a precise line between them. The shells are of moderate size, as a rule a little smaller than those of *bengalensis*. The whorls are more contracted and not so convex in outline, distinctly flattened as a rule outside the suture; the aperture is smaller, narrower and more pointed above and the umbilicus still narrower. The body-whorl often shows a tendency to become biangulate and the dark bands are sometimes incrassated. The colours are usually rather deep, but dull, and the bands are well developed.

The "normal" type of shell is much the commonest, but the "elongate" type occurs occasionally.

Type-series. No. M5080/1 *Z.S.I.*

Geographical Range.—The range extends from the Nepal valley along the base of the Eastern Himalayas as far east as Siliguri, below Darjiling. At or near this point the race merges into the Assamese race *balteata*. Specimens from Gauhati on the Brahmaputra, however, belong to it rather than to the latter. They are much more brightly coloured than specimens from Nepal.

I found the race common in ponds with submerged and floating vegetation at Gauhati.

Race **balteata** (Benson).

(Plate I, fig. 8.)

1836. *Paludina bengalensis*, var. *balteata*, Benson, *Journ. As. Soc Beng.* pt. 2, p. 745.
1909. *Vivipara* (*bengalensis* var.) *balteata*, Kobelt, *op. cit.*, p. 415, pl. lxxvii, figs. 11-12.

Were all the shells of this race like the one figured by Kobelt, there would be little doubt as to the propriety of regarding it as specifically distinct; but his figure represents an extreme type, which, though common, is by no means universal in the race. My own figure (pl. I, fig. 3) represents a shell that goes almost to the opposite extreme. Both types are present in several series examined from Sylhet and the eastern parts of the Brahmaputra valley. It will be noticed that Kobelt's figure represents a small shell of the "elongate" type, mine a larger one of the "normal" type.

Most shells resemble the former. They rarely exceed 20 mm. in height and are narrow in proportion. The whorls are somewhat contracted, the aperture ovoid and the umbilicus closed. The dark bands are well developed and sometimes all of them are very narrow. They are frequently thickened and prominent. Shells of the "normal" type are often larger, with a very large sub-circular aperture. Their body-whorl is frequently almost biangulate, and the dark bands alternate in width. Intermediates between the two types are not uncommon. In both types, the shell is very thin and quite translucent when fresh. Specimens can often be found so similar to some of those of the Burmese race *doliaris* that they can hardly be distinguished from them. Others closely resemble Peninsular shells of the phase *annandalei*.

Geographical Range.—The headquarters of this race is the Sylhet valley in southern Assam, but it also occurs in the eastern part of the valley of the Brahmaputra. It is absent from Manipur. There are specimens in the Indian Museum labelled Siliguri but this is probably a mistake for Silcuri in Cachar, where Benson originally obtained specimens.

I am informed that this race is often found in flooded rice fields.

Race **doliaris** (Gould).

(Plate I, fig. 9.)

1843. *Paludina doliaris*, Gould, *Proc. Bost. Soc. Nat. Hist.* I, p. 144
1869. *Paludina digona*, Blanford, *Proc. Zool. Soc. London.*, p. 445.
1876. *Paludina digona*, Hanley and Theobald, *op. cit.*, pl. cxv, fig. 7.

The most characteristic feature of this race is the one described in Blanford's name *digona*. The biangulate outline of the body-whorl is due to the presence of two spiral ridges which are merely dark bands thickened, but this feature is not equally developed in all individuals and in some is almost absent. In typical specimens the aperture is exceptionally large and wide, the columellar edge prominent, and the umbilicus rather broad;

but these characteristics are inconstant, especially in shells of the "elongate" type, which are found not uncommonly. In both this and the "normal" type, however, the shell is relatively broader than in the corresponding types in the *forma typica*, and the upper surface of the whorls is more or less broadly and obliquely flattened; the dark bands, which have the typical arrangement, are as a rule slightly incrassated and the aperture is subangulate, at any rate to a slight degree, at its outer and lower extremity. The size is usually larger than that of *balteata* but a little smaller than that of the *forma typica*.

In some respects the three eastern races (*nepalensis*, *balteata* and *doliaris*) represent a developmental series and would seem to indicate that there has been a tendency for the species to develop along certain lines as it proceeds eastwards, notably in the assumption of dark spiral bands of a prominent character and the special development of two of these bands as keels. A similar line of development can also be traced, but less completely, in the Peninsular phases of the species.

Geographical Range.—The race *doliaris* has its headquarters in the valley of the Irrawadi, down which its range extends at any rate from Bhamo to the delta. It is also found on the lower Siltang and probably on the lower Salween.

Race **eburnea**, nov.

(Plate II, figs. 1–2.)

In this race the shell is as a rule slightly narrower than in the *forma typica* and its aperture smaller; the body-whorl is also less enlarged and does not project outwards to the same extent in dorsal view. The whorls are narrow but distinctly flattened outside the suture and the body-whorl sometimes shows a tendency to become biangulate. The longitudinal striae are very fine and as a rule more regular than in *bengalensis* (s.s.), and strong traces of spiral sculpture can nearly always be detected with the aid of a good hand-lens. The aperture of the shell is slightly pyriform and the umbilicus is very narrow if not completely closed. The shell-substance when fresh has an ivory-like appearance. The outer surface is lightly tinged with yellowish olive and the spiral bands are never very dark. Sometimes they are obsolescent, but traces of them can usually be found at any rate on the upper whorls and the alternating broad and narrow bands are often quite clear. Sometimes the dark bands coalesce on the body-whorl. The aperture never has a black rim.

Elongate shells are not uncommon and individuals intermediate between this type and the normal one occur more frequently than in the *forma typica*.

The animal in this race is pale olivaceous and has a peculiar translucent appearance, but the yellow spots characteristic of all races are never obsolete.

Type-series. No. M11960/2 *Z.S.I.* (from the Keligiri reservoir Nellore district, Madras).

Geographical Range.—This is the race commonly found in the large reservoirs of the Madras Presidency and the central parts of India. It occurs in abundance as far north as Sambalpur in the interior of Orissa and has been collected occasionally in the south central parts of the Ganges valley. Specimens from the northern parts of its range are nearer the *forma typica* than those from the eastern districts of Madras. Nevill states (*Cat. Moll. Ind. Mus.* p. 27) that the spiral bands are sometimes absent in specimens from near Calcutta, but such specimens are mere albinistic aberrations and do not resemble *eburnea* in other respects.

The race is usually found in perennial bodies of still water. It reaches its maximum development among algae growing on stones.

I include provisionally in this race a small series of specimens from a large pond in the town of Godaveri in the eastern part of Madras. The shells are similar in shape but have the suture more impressed. In one specimen, indeed, it is canaliculate, and so deep that it forms an actual break in the shell at certain points, where the soft parts are exposed; but this shell was evidently diseased. The pigmentation of the shell is very dense, the outer surface being blackish brown with only traces of the spiral bands, while the interior is deep blue. The animal was also very dark.

These specimens were found amongst dense masses of the Water Hyacinth and *Pistia stratiotes*, so congested that many of the plants were rotting. Their peculiarities may be due to this fact.

Race **colairensis**, nov.

(Plate I, figs. 5–6.)

This race is one of the most distinct with which I am acquainted. It is remarkable for the elongate form of the shell and its relatively small aperture, which is almost circular. These features are noteworthy both in the normal and the elongate type, which occurs rarely with the former. The shell is of very large size, but thin and somewhat translucent. The pigmentation is rather deep, but dull. The alternating broad and narrow bands are distinct. The sculpture resembles that of the *forma typica*.

Type-series. No. M11961/2 *Z.S.I.*

Geographical Range.—I know this race only from a single pond at the village of Sriparptipada on the edge of the swamps that skirt the Colair Lake in the Kistna district of Madras. Specimens from the lake itself belong to the race *eburnea*.

Habits.—The pond in which my type-series was obtained was deep and contained abundant water although the district was suffering from a very serious drought at the time of my visit (September, 1918). It had an abundant and healthy vegetation of submerged weeds and plants with floating leaves (Limnanthemum and water-lilies) were also abundant and healthy. The molluscs were taken among the leaves in great profusion. Their habitat was of a type more common in Lower Bengal than in Madras.

This exhausts the number of true races with which I am acquainted and we may now turn to the four well-marked phases of the species.

Phase annandalei, Kobelt.

(Plate II, figs. 5–8.)

1908. *Vivipara annandalei*, Kobelt, *Nachr. Malak. Ges.* LX, p. 161.
1909. *Vivipara annandalei*, Kobelt, in Martini and Chemnitz, *Conch. Cat.* I, 21 (2), p. 296, pl. 57, figs. 11, 12.

Kobelt refers to this form as "*eine kritische form.*" I was prepared to accept it as distinct until I had become acquainted with its habits and had ascertained the fact that in some ponds (*e.g.* the tank in the Museum compound, Calcutta) it graded insensibly into the typical form of *V. bengalensis*, or rather into a small but not otherwise peculiar phase thereof. Kobelt's description and figures were based on somewhat exceptional specimens of relatively large size and proportionately broad shell. Such individuals occur occasionally but are by no means typical of the phase. On pl. II four shells are shown. Fig. 5 represents one of Kobelt's type-series, which is from Vizagapatam in the north-east of Madras. The other three (figs. 6–8) are more typical. The shells examined by Kobelt were, moreover, old specimens and had lost the translucency characteristic of the phase.

The shell is always very thin and light and usually small. The more elongate type is the commoner of the two that occur, but the type-series chances to belong to the other. Apart from the thinness and translucency of the shell, the most characteristic features are the gradual increase in size of the whorls, the shallowness of the suture, and particularly the shape of the aperture, which is distinctly subrhomboidal and subangulate at its anterior extremity. The dark bands are sometimes a little incrassated. Some shells of the phase come very near to some of the Assamese race *balteata*. The animal is usually very pale in colour, but occasionally almost as dark as that of the *forma typica*. I have noticed that in living specimens kept in an aquarium it gradually becomes darker.

This phase is found in the territory both of the *forma typica* and of the race *eburnea*, but I can find no difference between specimens from Calcutta and those from Hyderabad, Deccan. It is commoner in the vicinity of both cities and almost always occurs in pools of rather foul water used for domestic purposes.

Phase **halophila**, Kobelt.

(Plate II, figs. 9, 10.)

1908. *Vivipara annandalei halophila*, Kobelt, *op. cit.*, p. 162.
1909. *Vivipara annandalei halophila*, Kobelt, *tom. cit*, p. 297, pl. 59, figs. 17-20.

The type series of this phase was noted by Nevill as 'a short angulate form, almost indistinguishable from some of the Burmese var. *doliaris*.' It resembles *annandalei* very much as *doliaris* does *baltcata*, but is certainly not a local race. The type-series was from the Punjab Salt Range, but I have also examined series from Calcutta and Burdwan in Bengal. The shell has a distorted appearance and is usually eroded at the tip. Its sculpture is coarse and irregular, the dark bands are usually incrassated and the body-whorl frequently sub-biangulate. The aperture resembles that of the shell of *annandalei*, but is usually larger and broader.

In calling this form *halophila*, Kobelt referred to the name of the locality of the type-series, but it is by no means improbable that the phase does live in water of abnormal chemical composition. Unfortunately I have never found it living myself.

Phase **incrassata**, nov.

(Plate II, figs. 3, 4.)

Shells of this phase differ from those of the race *eburnea* in being very thick and opaque and in having as a rule coarse irregular varices on the body-whorl. They are often almost devoid of pigment. Sometimes the umbilicus is more open than usual. I have examined a good series from Poona in western and from the Kurnool district in southern India. Unfortunately I know nothing of its habitat, but it resembles *eburnea* so closely in all but the thickness and sculpture of the shell that it can hardly be more than a phase of that race.

Phase **pachydolicha**, Annandale.

1921. *Vivipara bengalensis* phase *pachydolicha*, Annandale, *Rec. Geol. Surv. Ind.*, LI, p. 367, pl. xi, figs. 5-7.

I assign to this phase certain large elongate shells in which the umbilicus is more open than usual, and the mouth small and oval. The whorls are swollen and the sculpture impressed, with the upper surface of the whorls broadly and obliquely, but somewhat obscurely flattened, just outside it. There are numerous distinct minutely sinuate, spiral striae on the surface, and the longitudinal striae are coarse and irregular. The epidermis is a dark olivaceous brown in colour with numerous longitudinal black streaks. The spiral bands are narrow and obscure.

I have seen only two fresh specimens of this phase, but there is a series of fine subfossil shells in the collection of the Geological Survey of India.

The fresh shells were found on the sea-shore at Puri in Orissa near small pools of fresh water in the almost dry bed of a stream, the mouth of which was temporarily blocked. The subfossil specimens are from the alluvium of the Narbadda.

I should have regarded this phase as specifically distinct, were it not for the fact that some specimens of the phase *incrassata* approach it closely. It is probably another modification of the race *eburnea*.

PART IV.—BIONOMICS.[1]

By R. B. SEYMOUR SEWELL.

The Life-history.

The breeding season of *Vivipara bengalensis*, that is to say the period during which the young are born, commences early in the year and seems to extend throughout the whole of the hot-weather and monsoon periods up to and probably beyond September; but the period of most intense reproduction is from April

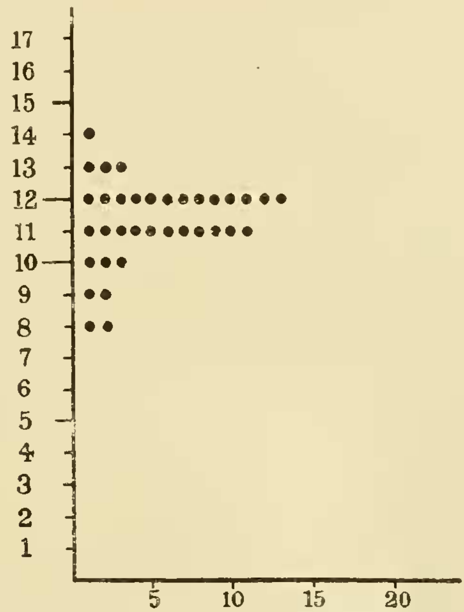

FIG. 20.—Length measurements of 35 examples of young *Vivipara bengalensis*, born in experimental tanks, at the age of 3 months old.

to July. During this period the uterus of a mature female is crammed with eggs, containing young in varying stages of development, but young Viviparidae are to be found *in utero* at all seasons of the year. I have even found them to be present in examples that had buried themselves in the mud at the bottom of a tank in Lahore at the onset of the cold weather and were dug up in December. Examples of *Lecythoconcha lecythis*, dug from

[1] In compiling this section I am greatly indebted to Dr. Annandale for many additional notes and observations.

dried mud at the edge of a swamp in Manipur, and brought to Calcutta in March, produced living young when placed in water.

Newly born examples of *V. bengalensis* are comparatively well-developed and already show 3½ turns of the spiral in the shell. In a preceding part of this paper Dr. Annandale has described the young shell.

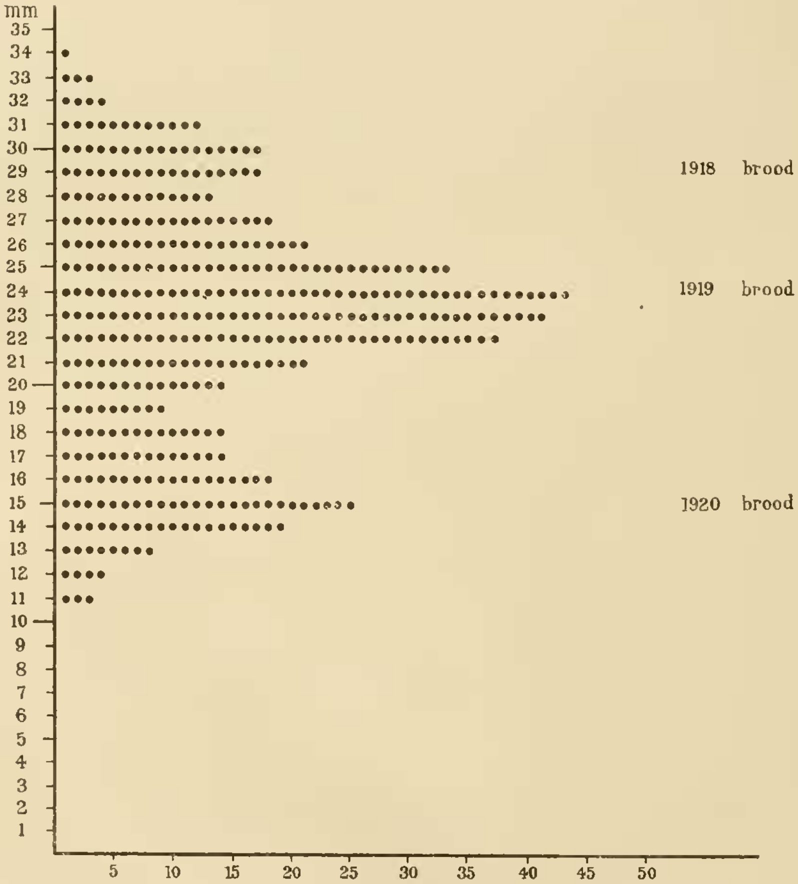

FIG. 21.—Length measurements of 409 examples of *Vivipara bengalensis*, taken from the tank in the Indian Museum compound, July 26th to August 2nd, 1920.

Growth at first proceeds rapidly. Newly born individuals measure approximately 3 mm. in maximum height from the apex of the shell to the margin of the peristome, but in less than three months a complete extra whorl has been added and the height of the shell is now approximately 15 mm. During May and August, 1919 a number of examples of *Vivipara bengalensis* were kept under observation in experimental tanks in the Indian Museum. These adults were introduced into the tanks between the 2nd and 23rd of May, 1919. Young were deposited in large numbers and at the end of July several were collected and measured, and the results obtained are given in fig. 20. The measurement taken was the maximum height as defined above, and the individuals fall into a well-defined regular group, the measurement ranging from 8 mm. to 14 mm. and having an average of 11·3 mm. Since all these examples were less than three months old, we get some idea of the very rapid growth that takes place in early life. At the same time a number of adult examples from the pond in the Museum compound were measured and were found to fall into a group having a length measurement of 20 mm. to 27 mm. This I believed to represent the size attained after one year of life, and, in order to check this, between July 26th and August 2nd, 1920, 409 examples from the same pond of all sizes except the very smallest, which had obviously only recently been born, were collected and measured. The results are given in fig. 21. It will be seen that we have two well-defined groups with their maxima corresponding to a height measurement of 15 mm. and 24 mm. respectively.

The members of the first group correspond very closely both as regards size and degree of development with the examples hatched and reared in the experimental tanks in 1919. They are somewhat larger, but the experiments of Semper (1874), De Varigny (1894), and others have shown that growth is more rapid under favourable conditions and in large areas of water with efficient natural aeration than it is under artificial conditions in small aquaria, and it seems reasonable to conclude that the individuals comprising the group of the 1920 brood were approximately three months old and had been born about April. This rapid rate of growth, from 3 mm. in height when born to 12–15 mm. at approximately three months, corresponds closely with the results obtained by Lyon (*vide* Baker, 1911, p. 51) in which examples of *Limnaea* (*Galba*) *reflexa*, measuring 2·00 mm. at 6 weeks old, attained to a height of 5–10 mm. at 12 weeks and 26·0–28·5 mm. at one year old, or by Woodruff (*loc. cit.*) who found that examples of *Limnaea* (*Radix*) *auricularia* increased from 0·75 mm. in height when born to 11·50 mm. at 4 weeks. As age progresses, the rate of growth naturally becomes slower, since other and equally important processes are going on in the young individual, especially the attainment of sexual maturity.

The second group, having an average height of 24 mm., corresponds exactly with the adult examples taken from the pond in August, 1919.

It seems clear that these two groups of *Vivipara bengalensis* correspond respectively to the 1919 and 1920 broods, but there are indications of a still further group having an average height of 29–30 mm.; this however does not appear very clearly in the chart owing to overlapping with the group of the 1919 brood. These large individuals, which were much fewer in number than those of the preceding group, I take to represent individuals who have survived for a further period of one year and who represent the

1918 brood. The great majority of these large examples show a well-marked 'varix' across the middle of the body-whorl of the shell, thus indicating that there has been a period of arrested growth followed by a subsequent increase in size. The distance from the apex of the shell to the umbilical end of the varix measures approximately 24 mm. which corresponds closely to the average height attained by examples that are one year old, and it is evident that the period of arrested growth corresponds to the second winter of their life-history. The maximum length of life of any individual appears then to be two years, but the vast majority of individuals die after one year. Each year towards the end of the rains there is a very heavy mortality among the molluscan fauna of the ponds and tanks, etc., in this country. This was first noticed in a period of exceptional drought by Dr. Annandale, who called attention to it in his preliminary report to the Government of India on the mollusc survey of the Madras Presidency, but he attributed it to the partial drying up of the pools and the consequent foulness of the remaining water. The same mortality, however, occurred, though perhaps on not quite so large a scale, in ponds in Calcutta in August, 1919, where no such causative agent could be suspected, and it appeared to be a natural phenomenon affecting many different genera of molluscs, including *Vivipara*.[1] In *V. bengalensis*, the vast majority of individuals born in the preceding year die during this period, only a few surviving for a second year. This heavy annual mortality among the freshwater molluscs is a phenomenon of considerable antiquity, for Annandale (1920 (*a*), p. 53) has adduced evidence that it was in existence in the Intertrappean (late Cretaceous) beds of this country.

The sexual differences in the antennae of *Vivipara bengalensis* render it easy to carry out an investigation regarding the influence of sex on the individual. I have been quite unable to detect any difference in the shape of the shell, but measurement of a number of individuals of both sexes, collected haphazard from the pond in the Indian museum compound[2] shows very clearly that there is a quite appreciable difference in height. In fig. 22, I have given the measurements of 147 female and 57 male examples and it shows that the average height of females of one year old is 25·0 mm. and of two years old 30·0 mm., whereas males of the corresponding length of life have an average height of only 22·0 and 27·0 mm. respectively.

Difference in size in the two sexes of *Vivipara vivipara* was noticed as long ago as 1695 by Lister, and more recently Wood-Mason (1881, p. 86) has recorded the same sexual character in

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[1] *Vide* Annandale and Sewell "Progress report on a Survey of the Freshwater Gastropod Molluscs of the Indian Empire and of their Tremetode Parasites." *Ind. Journ. Med. Research* VIII, p. 119.

[2] Examples living in this pond are considerably smaller than those found in certain other localities.

examples of *Vivipara crassa* (Hutton) that he obtained and examined in Sylhet. This difference in size is also known to occur in other genera and according to Cooke (1895, p. 134) "is markedly the case in *Littorina, Buccinum,* and all the *Cephalopoda.*" It is generally assumed that the difference in the two sexes is related to the viviparous habit and is dependent on the necessity for

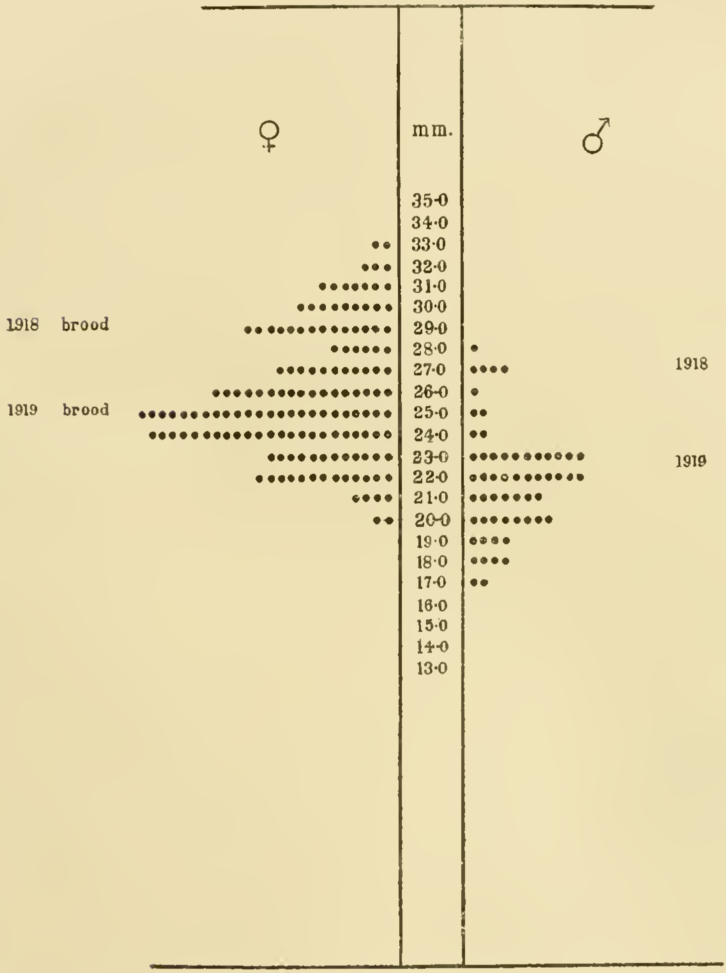

FIG. 22.—Measurements of 147 ♀ examples and 57 ♂ examples of *Vivipara bengalensis.*

increased space in the shell of the female in order to accommodate the large numbers of contained young in utero. If this were the sole causative agent, one would expect to find the condition constantly present, but this expectation is not fulfilled in the Viviparidae of this country, for in certain species no difference can be detected in the two sexes, while in others there is a difference in the shape of the shell though not in height. In *Vivipara oxytropis* (Benson) Annandale found that while there was no difference in the height of the shell of the two sexes in the adult, the female shell was considerably broader than the male. In *Lecythoconcha lecythis* (Benson) also large shells were of the same height, but the whorls of the spire increased in size more gradually in the female. In the genus *Taia* Annandale (1918, p. 137) found that there was very little sexual variation in the shell in *T. intha*, though he found specific differences in sexual variation in the genus as a whole. In *Lecythoconcha* and *Taia* the young *in utero* are relatively large as compared with *Vivipara bengalensis* but this is not so in *V. oxytropis*. It appears probable, therefore, that there is some reason other than the mere necessity of increased space for the accommodation of young to account for this difference in height of the shell in the two sexes, and a possible cause may be found in the natural antagonism between bodily growth and the attainment of sexual maturity. In *Vivipara bengalensis* and probably in many other species of mollusc in this country sexual maturity is attained at a very early date. Whitfield (1882) states that examples of *Limnaea* (*Bulimnaea*) *megasoma* Say, which he hatched out from the egg and managed to rear successfully in the United States, America, became sexually mature at the age of one year. According to Baker (1911, p. 50) "the duration of life in the family Limnaeidae is from three to four years, full maturity being reached in about two years," and though I have no information regarding other genera in temperate regions it is probable that they much resemble the Limnaeidae in this respect. In this country and in Egypt, however, the general condition is vastly different. Manson-Bahr and Fairley (1920, p. 65), who were engaged in investigations regarding Schistosomiasis in Egypt, state that in that country examples of *Bullinus* and *Planorbis* become sexually mature at the early age of three months, and the same undoubtedly occurs in examples of *Vivipara bengalensis* in India. Dissection of fifty examples belonging to the 1920 brood, during July, showed that already many of them were sexually mature, and this was especially so in the males. In many cases the gonad was well developed and was full of ripe spermatozoa. In the females, only comparatively few were sexually mature. The smallest sexually mature male measured 13 mm. in height, while the smallest female with eggs and young *in utero* was 16 mm. Two others of the same height had a quantity of seminal fluid in the egg-shell gland, so that copulation had taken place. Assuming that the rate of growth is equal in both sexes up to the onset of sexual maturity, it would appear that the males become mature at an earlier date than the females, and the antagonism between growth and the attainment of sexual maturity occurs when the males are smaller, thus producing a disparity in size between the two sexes. In spite of their increased bulk females of the age of two years are remarkably less fertile than those of only one year old. In only three examples out of a total of fourteen belonging to the 1918 brood and examined by me in August, 1920 were eggs, in which development was in an early stage, found *in utero*; in five others the uterus contained a few embryos in a comparatively advanced stage, with 3 to 3½ whorls in the spire; and in the remaining seven the uterus was empty. The average production of these examples was 2·8. On the other hand nine females belonging to the 1919 brood yielded an average of 12·0 eggs or developing young, so that in spite of their greater size, examples of the age of two years show very distinct evidence of senile decay, and it is not improbable that in many cases the young offspring found *in utero* had been retained since the previous breeding season.

Under certain conditions of cold, drought, etc., *Vivipara bengalensis* appears to be capable of undergoing 'hibernation.' In December, 1919 I examined a series of examples that had been obtained during that month by Mr. Sunder Lal Hora from the mud, in which they had buried themselves, at the bottom of a pond in Lahore. In every case the uterus contained a certain number of live young, which must obviously have been the product of the previous breeding season, and which would doubtless have been set free during the following season, in the event of the parent having been able to survive. Annandale has pointed out that *V. bengalensis* is less modified, especially in the structure of the operculum, for resisting drought than the species of the *V. dissimilis* group (sub-genus *Idiopoma*, Pilsbry). In a bottle full of specimens of *V. bengalensis* and *V. dissimilis*, recently brought to Calcutta from the Ganjam district of Madras, the difference in the behaviour of the two species as the water became foul was very marked. The individuals of *V. bengalensis* crowded round the edge at the top of the water with the aperture of the branchial chamber above the surface and widely open, as though inhaling air, while those of *V. dissimilis* closed their opercula tightly and sank to the bottom.

A further interesting point brought out by a study of the two sexes is the greater mortality among males during the period following the attainment of sexual maturity. Out of the fifty examples of the 1920 brood that were examined the proportion of the sexes was 24 ♂ and 26 ♀, so that at this period of life the numbers are approximately equal. A reference to fig. 21 shows that at the end of the first year of life the proportion of the sexes was 203 ♀ to 51 ♂ or roughly 4 : 1. While at the end of the second year of the life the proportion had become still greater and there were as many as 44 ♀ to 6 ♂ or 8 : 1. Wood-Mason (1881, p. 87), when examining a series of examples of *Vivipara crassa*, found that in seventy-six specimens forty-six were females and only thirty were males. He was, however, doubtful whether this difference in the numbers was due to an actual minority in the males or was merely the result of his collector having naturally tried to secure the largest possible specimens, but in view of the figures obtained by me in *V. bengalensis* I am inclined to believe that we get a similar disproportion of the sexes in both these species. This disparity in numbers is not, however, of universal occurrence in the Viviparidae for Dr. Annandale informs me that in the Loktak Lake adult females of *Lecythoconcha lecythis* were at least as numerous as adult males, whereas in the case of *Vivipara oxytropis* females were distinctly less numerous than males.

As I have already mentioned, examination of 50 examples of the 1920 brood in July, taken from the pond in the Indian Museum, showed that the proportion of ♂ to ♀ was 24 : 26. A further examination of 35 examples from the same source in August gave a corresponding proportion of only 15 : 20, so that there had already been a considerable drop in the proportion of ♂ examples present. I give below a table showing the proportion of the two sexes in individuals of different sizes.

TABLE I.—*Showing the proportion of sexes in individuals of different sizes from the pond in the Indian Museum.*

Length of shell.	11 mm.	13 mm.	14 mm.	15 mm.	16 mm.	17 mm.	18 mm.
♀	3	3	2	5	4	2	1
♂	1	...	1	1	5	4	3

This shows clearly that in the larger examples the proportion of ♂ sex is high whereas the exactly opposite condition prevails among the smaller examples. We have already seen that individuals of 11 mm. in length are of an age of three months or less, and these must therefore have been born about the beginning of June, whereas those having the greater length of 18 mm. were almost certainly born in April or earlier. It seems clear then, that at the commencement of the breeding season there is a very distinct tendency to produce ♂ offspring, whereas later in the season it is mostly ♀ examples that are produced. I am inclined to attribute this alteration in sex-production to the variation in external conditions. I know of no data that would enable one to form an estimate of the length of the period of gestation, during which the developing embryo is retained within the uterus, and it probably varies at different periods of the year, but it seems likely that offspring born in April are derived from ova that became mature and were fertilized during the winter season, whereas offspring born later in the year will be derived from eggs that became mature during the warmer weather. If this be so, we have here another example of the influence of adverse surroundings in the production of male offspring.

Food.

A study of the contents of the stomach of a number of examples, as well as observations carried out on living specimens, show that the normal food of *Vivipara bengalensis* consists almost entirely of algae and minute particles of vegetable matter which are rasped off from the surface of submerged plants, stones, decaying vegetable matter, etc. Along with these fragments of vegetable origin, a considerable quantity of fine mud and sand is ingested and swallowed in consequence of which the bulk of faecal material is very large. After passing up the oesophagus the food is mixed in the stomach with the bile which is poured out by the hepatic ducts, so that the stomach contents have a brown appearance and are liquid in character. As the contents are passed down the intestine, they become more and more solid and are finally moulded into small oval pellets which are at first usually rounded at one pole and more or less acutely pointed at the other. Later on, however, both poles become rounded. Finally these pellets are ejected through the anus into the syphonal tube and are forcibly swept out of the body by the outflowing current of water.

At times individuals have been found whose stomach and intestine were crowded with enormous numbers of a species of *Volvox*. These invariably contained within the parent colony a number of daughter colonies, and it is interesting to note that although the superficial cells of the parent colony were digested, the daughter colonies, being more deeply seated, entirely escaped digestion, and passed out of the body in the faeces in apparently a perfectly healthy condition. Gravely (*vide* Annandale, 1911, p. 216) has noted a somewhat similar phenomenon in the fresh-water polyzoon, *Plumatella repens*.

If aquatic vegetation is not available, as was the case where examples were kept in earthen basins or glass bowls, the animals could frequently be seen rasping off the algae that were growing on each others shells.

Although normally vegetable feeders, this *Vivipara* is by no means averse to a carnivorous diet, and feeds on the bodies of other dead snails. This habit appears to be by no means uncommon in molluscs that are normally vegetable feeders. Benson (1829, p. 363 and 1830, p. 126) has called attention to the carnivorous habits of a species of *Paludina*, under which generic term *Vivipara* was formerly included, but from his description of the animal it seems probable that he was referring to a species of *Bithynia* or *Amnicola*. Baker (1911, p. 42) has also pointed out that *Limnaea* is at times carnivorous though normally a vegetable feeder, but his statement that " the part they play as natural scavengers renders their presence in water-troughs and other sources of drinking water highly desirable " seems to overlook the fact that the presence of these snails may be and almost certain would be highly dangerous as a source of trematode infection.

More recently Annandale (1920 (*b*), p. 1) has noted that *Pachylabra* (Ampullariidae) is occasionally carnivorous.

Parasites and Incolae.

Amongst the normal inhabitants of the alimentary canal of *Vivipara bengalensis* and probably of other species of the same genus are several different types of ciliate protozoa, and it seems worth putting on record that in almost every individual examined. I have found what appear to be Spirochaetes in both stomach and intestine. There appear to be two different forms. One of these measured 0·026–0·028 mm. in length and shows 6–7 curves in the spiral; it is highly refractile and quite easily seen under a high power. It moves backwards or forwards with equal facility. At times individuals are met with which show a narrow thin portion in the middle of their length, while short individuals having a length of 0·014 mm. and only 3 curves in the spiral are occasionally met with. It appears that these short forms are produced by transverse fission of the larger individuals. The second form of Spirochaete occurs in the rectum and measures 0·014–0·016 mm. in length; it is of a robust type and has two or three wave like bends in the course of its length.

In addition to the above, there is a rich bacterial flora, consisting of diplococci, rod-like bacilli, etc., in both stomach and intestine.

Vivipara bengalensis rarely acts as the *primary* mollusc host for the development of Trematodes. In this respect it forms a marked contrast to other species of the same genus, for *Vivipara fasciata* Müll. has been recorded as the primary host of nine different cercariae, and *V. vivipara* (L.) harbours as many as eleven. Out of a total of 283 examples of *V. bengalensis* I have only succeeded in finding cercariae on two occasions and in both individuals it was the same form that was present. This cercaria belongs to the group of Xiphidiocercariae, and was developing in small oval sporocysts.[1] In both cases the host was a male and development was taking place in the testis.

On the other hand, it is often extremely difficult to find an example that is not acting as an intermediate host. Two kinds of Agamodistomes[2] infect and become encysted in this species and each has a very distinct anatomical distribution. One type of cyst, which is circular in shape, is found in the auricle of the heart. These cysts enclose a stage in the development of an Echinostome. The other cyst is found in the gill-bars, it is oval in shape, and usually of a pale brown colour and enclosed within it is a small Agamodistome, that judging from its structure is derived from a Xiphidiocercaria. I am unable to say whether this Agamodistome represents a further phase of the life-history of the cercaria noted above, but the two are extremely closely related and both possess

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[1] For a description of this Cercaria see Sewell, "Cercariae Indicae," *Indian Journal of Medical Research* (in the press).

[2] Dollfus (*Mem. Soc. Zool. France* XXV, p. 87, Paris, 1912) has introduced the term 'Metacercaria' to describe the stage in the life-history of a Trematode between the free-living cercaria and its final establishment in its definitive host.

exactly the same type of excretory system. Infection with these two cysts appears to occur in different stages of the life-history of the mollusc host. Even in examples of so early a stage as 10 mm. in length, the gills have already become infected with the cysts of this Xiphidiocercaria; and out of 36 examples examined of sizes ranging from 10 mm. to 18 mm. in length only two were apparently free from this parasite. With regard to the Echinostome cysts in the auricle, however, infection appears to occur much later, and further the proportion of infection is extraordinarily different in the two sexes in early life.

TABLE. 2.—*Showing the percentage infection with Echiniostome cysts in the two sexes of examples of* 1920 *brood.*

Sex.	No. examined.	No. infected.	Percentage of infection.
♂	39	24	61·5 %
♀	46	15	32·6 %

The table shows that infection is twice as frequent in young males as it is in young females. No case of infection was found in examples that measured less than 14 mm. in shell length. I have already mentioned that sexual maturity is attained in this species when the individuals reach approximately the length of 13 mm. in the ♂ and 16 mm. in the ♀. Manson-Bahr and Fairley (1920, p. 66) have stated, and my own observations on the cercariae of this country have corroborated their statement, that "snails do not become infested with cercariae till they have reached maturity, that is about the third month." I have elsewhere put forward the view that infection by miracidia is probably largely dependent on the establishment of a chemotactic stimulus at the time when sexual maturity is attained in the mollusc host, and it seems possible that we are dealing here with a similar phenomenon. Certainly such an explanation would account for the higher percentage of infection in the males, which become sexually mature at an earlier stage of their life-history than do the females, and would also account for the freedom of infection of young immature examples. On the other hand infection of these molluscs by the Xiphidiocercaria and the production of cysts in the gill-filaments shows no evidence of any such phenomenon.

Turning now to the presence of these cysts and the degree of infection in adult individuals of either sex, I have given in the table below the results obtained from a careful examination of fifty examples, 25 aged 1 year and 25 aged 2 years. The point to which I wish to call attention is the very large percentage of ♂ examples that show a heavy infection with both Xiphidiocercaria and Echinostome cysts at the end of the 1st year of life, whereas at the end of the second year there is no such distinction between the two sexes. In cases where infection is heavy the auricle is so packed with cysts that it is a matter for wonder that it is able to perform its function at all, and in the case of the gills their physiological activity must be very seriously interfered with, leading to impaired vitality and a lowered resistance to adverse conditions. It is not improbable that we have here, if not the sole explanation, at least a contributory cause towards the marked progressive reduction in the proportionate numbers of adult males during the period of life succeeding the attainment of sexual maturity that, as we have already seen, occurs in this species.

TABLE 3.—*Showing the degree of infection present in adult examples aged one and two years.*

Degree of Infection.	AGAMODISTOME CYSTS IN GILL-FILAMENTS				ECHINOSTOME CYSTS IN AURICLE.			
	1st year.		2nd year.		1st year.		2nd year.	
	♂	♀	♂	♀	♂	♀	♂	♀
Absent	8%	13%	...	...	46%	42%	50%	30%
Slight	8%	31%	50%	47%	8%	48%	25%	45%
Heavy	84%	56%	50%	53%	46%	10%	25%	25%

The occurrence of Echinostome cysts in the auricle is by no means restricted to *Vivipara bengalensis*, nor is it confined to any particular district or country. Filippi (1855, p. 345) has recorded the occurrence of similar Echinostome cysts in the auricle of *Vivipara vivipara*, and he has further noted "qu'il ne m'a jamais été possible de voir la moindre trace de ces parasites dans les foetus des Paludines ; mais que les jeunes individus, pourvu qu'ils aient vécu quelques mois en liberté dans l'eau du lac en sont déjà enrahis.'' His results obtained in Europe agree, therefore, closely with the observations made in India. The occurrence of these cysts has also been noted by Moulinié (1886, p. 193).

As regards the geographical distribution in India, I have found these cysts present in examples of *V. bengalensis*, taken from five different areas of water in the Calcutta district. It is worth noting, however, that in examples of the phase *annandalei*, taken from a tank in Baliaghatta, this infection was absent in ten specimens that I examined : other examples from the same source were placed in experimental tanks, and when they were examined about 2 months later in every case cysts were present, so that infection had occurred during their sojourn in the experimental tanks. Extremely similar, if not absolutely identical cysts were found in identically the same situation, namely the auricle, in two out of six examples of *Vivipara dissimilis* taken from swamps near Bombay, and in nine out of eighteen examples of this species taken from a small ditch at Rambha, Ganjam; but in these latter cases the cysts were degenerating.

Yet another trematode may find a temporary resting place in Indian species of Viviparidae. Examples of *Lecythoconcha lecythis* and *Vivipara oxytropis* brought from the Loktak Lake, and of an undescribed species allied to *V. oxytropis* from Dimapore. Assam, were infected with trematode cysts in the mantle. These cysts were oval in shape, and were situated beneath the external or shell surface just behind the thickened mantle margin. The cyst-wall was thick and gelatinous and appeared to open by a single aperture on the shell surface of the mantle. Contained within these cysts were small examples of a species of *Urogonimus* Mont. [=*Leucochloridium* Carus]. I am elsewhere publishing an account of this species (*vide* Sewell, "Cercariae Indicae," *Ind. Journal Med. Research*); suffice it to say here that these trematodes measure 2–3 mm. in length, are of a deep orange-red colour and have a prominent ventral sucker with a diameter twice that of the oral sucker. Filippi (1855, p. 353, footnote) has recorded finding free distomes, which possess all the above characters, in examples of *Vivipara vivipara* taken from the Lake of Varese, Italy. As regards their distribution in the mollusc host he remarks, "Ils n'ont pas de place fixe, et souvent je les ai vu sur le manteau de l'animal." It is of course impossible to be certain on the point, but it seems by no means unlikely that he was also dealing with an intermediate stage in the development of a species of *Leucochloridium* in the European *Vivipara*.

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